AUSTRALIAN JOURNAL
OF BOTANY

VOLUME 2

MELBOURNE
1954

AUSTRALIAN JOURNAL OF BOTANY

Published by the Commonwealth Scientific and Industrial Research Organization, in collaboration with the Australian National Research Council, and under the general direction of the Editorial Board (Dr. N. S. Noble (Chairman), Professor J. S. Anderson, Professor Sir Macfarlane Burnet, Professor L. H. Martin, and Professor J. G. Wood). A medium for the publication of the results of original scientific research in botany with special emphasis on the descriptive phases

Issued as material becomes available, 7/6 per issue

EDITORIAL ADVISORY COMMITTEE

Chairman and Editor: Dr. N. S. Noble
Members: Dr. O. H. Frankel
Professor J. S. Turner
Professor J. G. Wood

All enquiries and manuscripts should be forwarded to:

The Editor,
Australian Journal of Botany,
Commonwealth Scientific and Industrial Research Organization,
314 Albert Street, East Melbourne, C.2, Victoria

MELBOURNE

CONTENTS

NUMBER 1, FEBRUARY 1954

PAGE

The Agrostological Index: A Phytogeographical Approach to the Problems of Pasture Plant Introduction. By W. Hartley .. 1

Radial Fissures in the Early Wood of Conifers. By G. L. Amos .. 22

The Effect of Wind Sway on the Form and Development of *Pinus radiata* D. Don. By M. R. Jacobs 35

The Cainozoic Occurrence of Acacia in Australia. By Isabel C. Cookson 52

The Fossil Occurrence of *Phyllocladus* and Two Other Podocarpaceous Types in Australia. By Isabel C. Cookson and Kathleen M. Pike 60

Autecology of Some Natural Pasture Species at Trangie, N.S.W. By E. F. Biddiscombe, E. G. Cuthbertson, and R. J. Hutchings 69

Botanical Contributions of the Northern Australia Regional Survey. II. Studies on Miscellaneous Northern Australian Plants. By S. T. Blake 99

Number 2, June 1954

PAGE

The Wood Anatomy of New Guinea *Nothofagus* Bl. By H. E. Dadswell and H. D. Ingle 141

Observations on Crossed Lamellar Structures in the Cell Walls of Higher Plants. By A. B. Wardrop 154

The Mechanism of Surface Growth Involved in the Differentiation of Fibres and Tracheids. By A. B. Wardrop 165

Aluminium Accumulation in the Australian-New Guinea Flora. By L. J. Webb 176

Some Dicotyledonous Pollen Types from Cainozoic Deposits in the Australian Region. By Isabel C. Cookson and Kathleen M. Pike 197

The Ecology of the Soil Fungi of an Australian Heathland. By Ethel I. McLennan and Sophie C. Ducker 220

The Rhizosphere Effect Shown by Some Victorian Heathland Plants. By L. B. Thrower 246

Corrigendum 267

NUMBER 3, NOVEMBER 1954

PAGE

The Leaf Anatomy of Australian Members of the Genus *Atriplex*. I. *Atriplex vesicaria* Heward and *A. nummularia* Lindl. By R. F. Black 269

Chromosome Numbers in the Boronieae (Rutaceae) and Their Bearing on the Evolutionary Development of the Tribe in the Australian Flora. By S. Smith-White 287

Objective Methods for the Classification of Vegetation. III. An Essay in the Use of Factor Analysis. By D. W. Goodall .. 304

A Quantitative Study of a Presumed Hybrid Swarm between *Eucalyptus elaeophora* and *E. goniocalyx*. By H. T. Clifford and F. E. Binet 325

Australian Species of *Sargassum*, Subgenus *Phyllotrichia*. By H. B. S. Womersley 337

New Soil Fungi from Australian Heathland: *Aspergillus, Penicillium, Spegazzinia*. By Ethel I. McLennan, Sophie C. Tucker, and L. B. Thrower 355

Corrigendum 365

Index to Volume 2 367

THE AGROSTOLOGICAL INDEX: A PHYTOGEOGRAPHICAL APPROACH TO THE PROBLEMS OF PASTURE PLANT INTRODUCTION

By W. HARTLEY*

(*Manuscript received July 17, 1953*)

Summary

In continuation of a previous study of grass distribution, a modified normal distribution spectrum is presented, giving the average percentage frequency of grass species of the five largest tribes in the eastern and western hemispheres. This modified spectrum forms the basis of iso-agrostological maps delimiting areas in which each tribe is present in more than normal frequency. An iso-agrostological map of the United States shows a general agreement with the distribution of temperature zones, but little correlation with vegetation.

More useful comparisons between grass distribution in different countries can be made through the agrostological index, in which the percentage of grasses in each tribe is included in one of 10 frequency groups. In general, areas in different parts of the world with identical agrostological indices have similar latitude, climate, and topography, though some exceptions are noted. Where accurate floristic data are available, the agrostological index may be used to show grass distribution in small areas, and the relationship of this distribution to climatic and other environmental factors.

Regions with similar agrostological indices have similar cultivated pasture plants, and hence the index may be of value in pasture plant introduction.

I. INTRODUCTION

In a previous study (Hartley 1950) the author has shown that the specific diversification of some of the larger tribes of the Gramineae throughout the world exhibits a regular pattern. Some tribes occur principally in the temperate regions, while others have most of their species in the tropics. The influence of climate in determining distribution is everywhere predominant, and it was postulated that "the number of species of any of the major grass tribes (excluding the Aveneae) in any region, expressed as a percentage of the total number of grass species present, bears a direct relationship to the climate of the region". The significant climatic factors vary from tribe to tribe, with temperature predominant in determining the distribution of the Agrosteae and Festuceae, while rainfall has an important influence on the distribution of the Paniceae and, to a minor degree, of the Eragrosteae. Historical factors have been important in determining the present distribution of the Andropogoneae and the Paniceae, the former being relatively abundant in the eastern hemisphere and the latter in the western hemisphere.

---

* Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T.

Since the publication of this paper many additional lists of grasses, from widely separated parts of the world, have become available, and in every instance these have helped to confirm the pattern of grass distribution previously described and mapped. The hypothesis quoted above has thus received further support, and it is possible to proceed with some confidence in using this relationship as an index of comparability of plant environment in widely separated regions and thereby as a useful guide in plant introduction work.

The present paper discusses a modified "normal spectrum" of grass distribution, the preparation of iso-agrostological maps, and the derivation and use of an "agrostological index" as a measure of similarity in plant environment.

II. THE MODIFIED NORMAL DISTRIBUTION SPECTRUM

It has previously been shown (Hartley 1950) that the average percentage of species of each of the major grass tribes in the grass flora of 64 localities widely distributed throughout the world is:

Agrosteae	8.2 per cent.
Andropogoneae	11.9 per cent.
Aveneae	6.3 per cent.
Eragrosteae	8.1 per cent.
Festuceae	16.5 per cent.
Paniceae	24.7 per cent.
Minor tribes (22)	24.3 per cent.

This is the "normal spectrum" of grass distribution, in the sense of Raunkiaer (1934). However, some modifications must be made in this normal spectrum before it can be used for the present purpose, viz. the comparison of plant environment in widely separated regions.

In the first place, the Aveneae should be omitted altogether, for evidence previously presented indicates that this tribe is taxonomically heterogeneous, and that this fact helps to explain anomalies in its present distribution. It is evidently not possible to use the distribution of a particular tribe as an indication of plant environment when the evidence suggests that its distribution is largely determined by non-environmental factors.

Secondly, some modification is required in the percentages given for the Andropogoneae and the Paniceae. While there is no evidence that these tribes are taxonomically heterogeneous or polyphyletic in the same way as the Aveneae, there is a clear indication that they are historically immature and have not yet achieved a balanced distribution throughout the world. As already noted, the Andropogoneae are relatively abundant in the eastern hemisphere and the Paniceae in the western hemisphere. Within each hemisphere there is little evidence of uneven distribution, except insofar as this can be accounted for by climatic and edaphic factors, but separate percentages must be used for each hemisphere if a useful comparison between them is to be possible.

For the Andropogoneae, temperature is the most important *climatic* factor determining distribution, rainfall having at most only a minor influence (Hartley 1950). On the world scale here under consideration, there is a general relationship between latitude and temperature, and it is therefore possible to obtain corrected percentages for the Andropogoneae by comparing their abundance in the western and eastern hemispheres in each latitudinal zone. The average percentages of this tribe for each latitudinal zone have been calculated for the localities used in determining the normal spectrum, with the results shown in Table 1.

TABLE 1

PERCENTAGES OF ANDROPOGONEAE IN THE TOTAL GRASS FLORA OF DIFFERENT LATITUDINAL ZONES

Latitudinal Zone	Western Hemisphere (*w*) (%)	Eastern Hemisphere (*e*) (%)	Ratio *e*/*w*
40-50°N.	1.3	2.6	2.0
30-40°N.	5.3	7.8	1.5
20-30°N.	8.4	19.1	2.3
10-20°N.	10.3	26.8	2.6
0-10°N.	13.0	23.6	1.8
0-10°S.	7.7	24.7	3.2
10-20°S.	9.3	29.2	3.1
20-30°S.	11.7	15.6	1.3
30-40°S.	9.9	7.7	0.8
			Mean = 2.1

Because of the small numbers involved and the effect of local variations in climate, it is not to be expected that the ratios given in the last column of Table 1 should show any high degree of uniformity. However, it appears reasonable to conclude that the percentages of Andropogoneae for the two hemispheres can be expressed as $An(e)/An(w) = 2.1$, where $An(e)$ and $An(w)$ are the "normal" percentages in the eastern and western hemisphere respectively. The normal percentage of Andropogoneae for the world as a whole, as given in the normal distribution spectrum, is 11.9. Taking this as the geometric mean the appropriate sub-values for the two hemispheres are:

$$An(e) = 17.2 \text{ per cent.} \quad An(w) = 8.2 \text{ per cent.}$$

In contrast with the Andropogoneae, rainfall is an important climatic factor influencing the distribution of the Paniceae, and consequently a comparison within latitudinal zones is not a satisfactory method of deriving sub-indices for the two hemispheres. In this instance, a comparison has been made between the percentages of Paniceae in localities in the two hemispheres with similar mean annual temperatures and mean annual rainfalls. The derived ratios again show considerable variation, but average values are $P(w)/P(e) = 1.8$, where $P(w)$ and $P(e)$ are normal percentages in the western and eastern hemispheres respectively. The corresponding value for Paniceae in the world spectrum is 24.7 per cent., so the sub-values are:

$$P(e) = 18.3 \text{ per cent. } P(w) = 33.3 \text{ per cent.}$$

No alterations are required in the values for the Agrosteae, Eragrosteae, and Festuceae, which have a historically mature distribution with little evidence of unbalanced distribution between the two hemispheres. The modified normal distribution spectrum for use in comparative studies thus becomes:

Agrosteae	8.2 per cent.
Andropogoneae (e)	17.2 per cent.
Andropogoneae (w)	8.2 per cent.
Eragrosteae	8.1 per cent.
Festuceae	16.5 per cent.
Paniceae (e)	18.3 per cent.
Paniceae (w)	33.3 per cent.

III. Iso-agrostological Maps

Using the modified normal distribution spectrum as a basis, it is possible to prepare iso-agrostological maps of regions for which adequate floristic data are available. Such maps show the zones in which each of the major grass tribes is present in greater frequency than in the modified normal spectrum.

To illustrate the method, an iso-agrostological map has been prepared for the United States of America (Fig. 1). This is based on the information on the distribution of each grass species by States throughout the country given in Hitchcock (1935), supplemented by more detailed information for Texas (Cory and Parks 1937). When the percentage of grasses of a tribe in any State exceeds the percentage in the normal spectrum by more than 10 per cent., that State has been included wholly within the zone of abundance of this tribe. When the corresponding percentage deviates from the normal percentage by less than 10 per cent., the demarcation line for the tribe has been drawn to pass through the State. Thus in Arizona and New Mexico the proportion of species of Agrosteae is more than 10 per cent. above the normal, while the percentages of Andropogoneae and Paniceae are below the normal. The proportions of species of Eragrosteae and Festuceae differ from the normal by less than 10 per cent., hence the line separating their zones of predominance passes through the States. In this way the subjective element involved in drawing the map has been reduced to a minimum, and the map is based almost exclusively on floristic data supplemented to a very minor degree by considerations of topography.

Inspection of this map, and comparison with climatic and vegetation maps of the United States, reveals several points of interest:

(i) While the iso-agrostological map demarcates adequately various zones in the eastern and southern parts of the country, very large areas in the north and west are all included in the Ag/F zone, which extends northwards to include the whole of Canada. In this respect it contrasts with some of the more generally used climatic maps (e.g. Koppen 1923; Thornthwaite 1931) which show greater differentiation in the west than in the south-east. This contrast is in part due to the more adequate representation of topographical effects in the climatic maps, but it is noteworthy that even the low-lying parts of the western United States (e.g. the Central Valley of California) fall within the Ag/F zone (data from Beetle 1947).

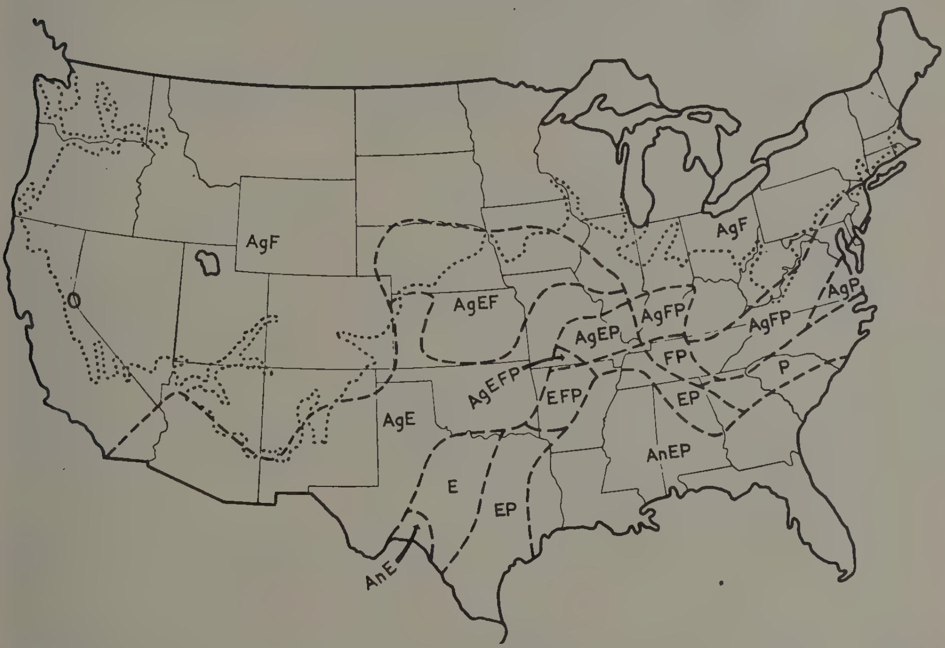


Fig. 1.—Iso-agrostological map of U.S.A. Ag, Agrosteae; An, Andropogoneae; E, Eragrosteae; F, Festuceae; P, Paniceae. . . . . . . Last killing frost after May 1.

(ii) The relatively greater importance of temperature as against rainfall in determining grass distribution is confirmed. In general, the dividing lines between the iso-agrostological zones tend to parallel the isotherms, though modified by the effects of rainfall (cf. Atlas of American Agriculture 1936). The effect of frost is important in some zones. Thus the boundary of the Ag/F zone corresponds very closely, except in

TABLE 2

ISO-AGROSTOLOGICAL DATA FOR AUSTRALIAN REGIONS, WITH ANALOGIES IN U.S.A.

Region	Reference	Percentages of Selected Tribes in Grass Flora					Iso-agrostological Classification	Analogues in U.S.A.
		Ag	An	E	F	P		
Kimberley District, W.A.	Gardner (unpublished data)	0	28.2	12.7	0	29.1	An/E/P	Louisiana, Mississippi, and Florida; southern Arkansas, Alabama, Georgia, and South Carolina
De Grey region, W.A.	Burbidge (unpublished data)	1.1	15.7	22.5	0	27.0	E/P	Rio Grande plain and Black-land prairies, Texas; north-eastern Alabama
South-western Queensland	Hartley (unpublished data)	4.4	10.6	23.0	0	18.6	E/P	
North-western slopes, N.S.W.	Turner (1903*b*)	2.8	9.4	15.9	9.4	23.4	E/P	
Western N.S.W.	Beadle (1948)	3.7	10.3	15.0	13.1	19.6	E/P	
New England, N.S.W.	Turner (1903*a*)	11.8	12.9	6.5	17.2	24.7	Ag/F/P	Southern Indiana; western Kentucky; eastern Tennessee; western N. Carolina and Virginia; Maryland
North-western Victoria	Field Naturalists Club of Victoria (1928)	10.4	5.2	7.9	22.2	17.7	Ag/F	Northern and western U.S.A.; south and east to Pennsylvania, W. Virginia, eastern Kentucky, northern Indiana, Illinois, and Iowa, S. Dakota, Colorado, western New Mexico, northern Arizona
North-eastern Victoria		16.6	6.5	3.6	26.0	12.9	Ag/F	
South-western Victoria		15.3	4.0	2.4	25.8	12.9	Ag/F	
Southern Victoria		15.3	3.0	3.0	23.7	17.8	Ag/F	
Eastern Victoria		12.9	4.3	3.4	25.0	16.4	Ag/F	
Southern S.A.	Black (1943)	10.4	4.5	2.0	26.0	9.7	Ag/F	
South-eastern S.A.	Black (1943)	14.7	3.2	1.0	27.4	11.6	Ag/F	
Tasmania	Rodway (1903)	21.2	3.0	2.0	27.3	4.0	Ag/F	
Far north, S.A.	Black (1943)	3.1	10.7	18.3	14.5	16.8	E	Central Texas, from Dallas to San Angelo and Laredo
Murray lands, S.A.	Black (1943)	5.4	6.4	10.7	19.3	17.2	E/F	No analogues

California, with the limit of the zone in which the average date of the last killing frost is later than May 1 (ibid, pp. 30-31). The anomalous position of California can be attributed to historical factors. The Sierra Nevada and the deserts of the Great Basin have acted as effective barriers against the spread of subtropical plants from the eastern United States into California, and there is thus a disproportionate representation of boreal floristic elements in the flora of that State (Campbell and Wiggins 1947).

(iii) There is very little correlation between the grass distribution zones and general vegetation zones in the United States (Shantz and Zon 1924). Some similarity can be traced in the eastern part of the country, where both iso-agrostological zones and vegetation zones have a similar north-east to south-west trend, but elsewhere the general east-west trend of the iso-agrostological zones contrasts sharply with the predominant north-south axis of the vegetation zones.

It is unfortunately not possible to prepare comparable iso-agrostological maps for most other parts of the world. Adequate and fully reliable information on grass distribution is wholly lacking for many important regions, and it is quite exceptional for such information to be available for large contiguous regions. Adequate data are available for the U.S.S.R., as Komarov (1934) records the occurrence of species in the 49 floristic zones into which the country is divided. From this information it is possible to calculate the percentage contribution of species of each of the major grass tribes to the total grass flora in each floristic zone. However, while there is considerable variation in the percentages from zone to zone, the predominance of the Agrosteae and the Festuceae is everywhere apparent, and the whole country falls within the Ag/F iso-agrostological zone. Thus the central and southern parts of the United States have no counterparts in the grass flora of the U.S.S.R. This conclusion is in accordance with the results of agroclimatic studies made by Nuttonson (1950). From a comparative study of meteorological data and crop distribution in Siberia and North America, Nuttonson concludes that the only parts of the United States comparable with any parts of Siberia are portions of Wisconsin, Minnesota, and North Dakota. These three States lie wholly within the Ag/F zone on the iso-agrostological map.

No recent floras are available for most of the Australian States, and there is a regrettable lack of reliable information on the distribution of grasses and other plants. It is therefore not possible to prepare an iso-agrostological map for the country, but in Table 2 the available information — some of it old and rather unreliable — is summarized and comparison made with the United States.

While it would obviously be unwise to place too much reliance on the data in this table, in view of the paucity and untrustworthy nature of the floristic information, it is noteworthy that the grouping of regions within

Australia and the analogues in the United States are in reasonable accordance with comparisons made on other bases. In some instances, the comparisons are too broad to be of real value. Thus the An/E/P zone is very extensively developed in the tropics, and the Kimberley district of Western Australia is not closely analogous to the south-eastern United States. Even here, however, it may be noted that the crop plants grown successfully in north-western Australia — e.g. rice and cotton — are also cultivated extensively in the portion of the United States classified as analogous. Similarly the Ag/F zone, as already noted, occurs throughout the cool temperate and cold parts of the world, and important differences in plant environment are found within this zone. Obviously the conditions of plant growth are different in Tasmania and in north-western Victoria. While the iso-agrostological map is useful for a rough visual assessment of similarities in grass distribution, it is unsuitable for more critical comparisons in zones of high or low latitude.

IV. The Agrostological Index

A more satisfactory and quantitative comparison between the grass flora of different places can be made by the use of the agrostological index. In the preparation of this index, the percentage values for each of the major grass tribes have been grouped into 10 classes. Thus the highest recorded value for the percentage of Agrosteae in the floras studied is 27.0 per cent. for the Dvina-Pechora region of the U.S.S.R. (Komarov 1934). The value of this percentage for any locality can thus be placed in one of the 10 classes listed below:

Class	Percentage of Agrosteae
0	0
1	0.1- 3.0
2	3.1- 6.0
3	6.1- 9.0
4	9.1-12.0
5	12.1-15.0
6	15.1-18.0
7	18.1-21.0
8	21.1-24.0
9	24.1-27.0

The limits of the classes for the other tribes are determined similarly and are shown in Table 3.

The grass spectrum for any locality can then be expressed as an "agrostological index" by using these classes. Thus the percentage of species of each of the tribes in the grass flora of the province of Santa Fe, Argentina (Ragonese 1941), is:

Agrosteae	2.3 per cent.
Andropogoneae	9.9 per cent.
Eragrosteae	6.9 per cent.
Festuceae	9.9 per cent.
Paniceae	42.7 per cent.

The agrostological index for Santa Fe is thus Agrosteae 1, Andropogoneae 5, Eragrosteae 3, Festuceae 2, Paniceae 6, or more shortly 1/5/3/2/6. Similarly for Mauritius, in the eastern hemisphere, with the percentages Agrosteae 0.7, Andropogoneae 23.0, Eragrosteae 8.6, Festuceae 2.9, and Paniceae 41.0 (Hubbard and Vaughan 1940), the agrostological index is 1/5/3/1/8.

TABLE 3

CLASSES AND CORRESPONDING PERCENTAGES OF GRASS SPECIES OF EACH TRIBE

Class	Percentage of Species of Each Tribe						
	Agrosteae	Andropogoneae		Eragrosteae	Festuceae	Paniceae	
		(East)	(West)			(East)	(West)
0	0	0	0	0	0	0	0
1	0.1- 3.0	0.1- 4.7	0.1- 2.2	0.1- 3.2	0.1- 6.2	0.1- 5.3	0.1- 7.3
2	3.1- 6.0	4.8- 9.4	2.3- 4.4	3.3- 6.4	6.3-12.4	5.4-10.6	7.4-14.6
3	6.1- 9.0	9.5-14.1	4.5- 6.6	6.5- 9.6	12.5-18.6	10.7-15.9	14.7-21.9
4	9.1-12.0	14.2-18.8	6.7- 8.8	9.7-12.8	18.7-24.8	16.0-21.2	22.0-29.2
5	12.1-15.0	18.9-23.5	8.9-11.0	12.9-16.0	24.9-31.0	21.3-26.5	29.3-36.5
6	15.1-18.0	23.6-28.2	11.1-13.2	16.1-19.2	31.1-37.2	26.6-31.8	36.6-43.8
7	18.1-21.0	28.3-32.9	13.3-15.4	19.3-22.4	37.3-43.4	31.9-37.1	43.9-51.1
8	21.1-24.0	33.0-37.6	15.5-17.6	22.5-25.6	43.5-49.6	37.2-42.4	51.2-58.4
9	24.1-27.0	37.7-42.3	17.7-19.8	25.7-28.8	49.7-55.8	42.5-47.7	58.5-65.7

From the examples given above it will be noted that the indices for Santa Fe and Mauritius are similar. The first three numbers of the two indices are identical, but Mauritius, as would be expected from its hotter climate, has a relatively lower index number for Festuceae and a higher one for Paniceae.

There are a large number of theoretically possible values of the agrostological index, but many of these are not encountered in nature. Thus high values for the characteristically tropical tribes — the Andropogoneae and Paniceae — are never combined with high values for the Agrosteae or Festuceae. In a total of 353 floristic lists which have been examined there are 205 distinct agrostological indices.

It is of some interest to note the areas in various parts of the world which have identical agrostological indices. These are shown in Table 4, excluding the British vice-counties, which are discussed more fully below.

It will be noted from this table that there is a progressive change from the tropical localities with characteristically low indices for the Agrosteae and Festuceae and high indices for the Andropogoneae and Paniceae, to those at high latitudes in the U.S.S.R. and elsewhere with high indices for the Agrosteae and Festuceae, and low indices for the Andropogoneae and Paniceae. This general trend is modified by the effect of altitude, for Peru and Ecuador, both predominantly mountainous countries in the tropical zone, have a fairly balanced representation of the tropical and temperate tribes.

In many instances, pairs or groups of localities with identical agrostological indices are contiguous. This is so for those American States with the indices 2/4/3/2/7, 2/5/4/2/7, 5/2/2/5/2, 6/1/1/6/1, and 6/3/3/3/2, as well as for some of those in the U.S.S.R. In such instances, geographical proximity and climatic similarity have resulted in substantial identity of flora, and the identity of the agrostological indices merely reflects this fact.

More interest attaches to the occurrence of identical indices in localities which are separated geographically. These may be in the same broad climatic zone and have many species in common, as exemplified by the insular and Mediterranean localities with the indices 3/1/1/7/2 and 5/1/1/7/1, or they may be more distant, and even in different hemispheres. The indices 0/6/4/0/8, 1/6/3/1/7, 2/3/3/3/4, 2/6/4/1/6, 4/1/2/5/2, 6/1/2/6/2, and 7/1/1/6/1 each embrace such widely separated regions. In general, the localities with identical indices occur within the same latitudinal zone and have similar climate, vegetation, and crop production. The resemblances between parts of the Malayan region and of the West Indies (index 1/6/3/1/7), between the eastern Cape Province and Buenos Aires (2/3/3/3/4), between Ceylon and Formosa (2/6/4/1/6), and between Patagonia, Wyoming, and parts of southern Siberia (7/1/1/6/1) need little emphasis. The only apparent anomalies are those involving the indices 4/1/2/5/2 and 6/1/2/6/2. These show that there is a similarity between the tribal composition of the grass flora of California and regions of much higher latitude and apparently dissimilar climate in the U.S.S.R. It has been noted, in discussing the iso-agrostological map of the U.S.A., that there is a disproportionate representation of boreal floristic elements in the flora of California. With these exceptions, it may be concluded that similarity in agrostological indices is closely associated with similarity in plant environment, at least insofar as this affects the growth and development of perennial herbaceous plants.

It will be noted that no Australian localities are listed in Table 4. In fact none of the Australian regional floras studied give agrostological

TABLE 4

LOCALITIES WITH IDENTICAL AGROSTOLOGICAL INDICES

Agrostological Index (Ag/An/E/F/P)	Locality	Literature Reference
0/6/4/0/8	British Honduras	Stanley and Record (1936)
,,	Gold Coast	Thorold (unpublished data)
1/6/3/1/7	Malay Peninsula	Ridley (1922)
,,	Java	Koorders (1911-37)
,,	Jamaica	Hitchcock (1936)
,,	Central Plain, Santa Domingo	Morosco (1943)
2/3/3/3/4	Uitenhage and Port Elizabeth, South Africa	Schonland (1919)
,,	Buenos Aires, Argentina	Parodi (1946)
2/4/3/2/7	Georgia, U.S.A.	Hitchcock (1935)
,,	South Carolina, U.S.A.	Hitchcock (1935)
2/5/4/2/7	Louisiana, U.S.A.	Hitchcock (1935)
,,	Mississippi, U.S.A.	Hitchcock (1935)
2/6/4/1/6	Ceylon	Willis (1911)
,,	Formosa	Kawakami (1910)
3/1/1/7/2	Balearic Is.	Knoche (1921)
,,	Canary Is.	Pitard and Proust (1908)
4/1/1/6/1	Western Kopet-Dag, U.S.S.R.	Abolin (1935)
,,	Tien Shan, U.S.S.R.	Komarov (1934)
4/1/2/5/2	San Diego Co., Cal., U.S.A.	Higgins (1949)
,,	Syr Darya foothills, U.S.S.R.	Komarov (1934)
4/3/3/4/5	Kentucky, U.S.A.	Hitchcock (1935)
,,	Maryland and Delaware, U.S.A.	Hitchcock (1935)
5/1/1/7/1	Greece	Halacsy (1900-08)
,,	Corsica	Briquet (1910)
,,	South Transcaucasia, U.S.S.R.	Komarov (1934)
5/2/2/4/5	Indiana, U.S.A.	Hitchcock (1935)
,,	Pennsylvania, U.S.A.	Hitchcock (1935)
5/2/2/5/2	North Dakota, U.S.A.	Hitchcock (1935)
,,	South Dakota, U.S.A.	Hitchcock (1935)
5/2/3/4/4	Illinois, U.S.A.	Hitchcock (1935)
,,	New York, U.S.A.	Hitchcock (1935)
,,	West Virginia, U.S.A.	Hitchcock (1935)
5/3/3/2/5	Peru	Macbride (1936)
,,	Ecuador	Hitchcock (1927)
6/1/1/6/1	Idaho, U.S.A.	Hitchcock (1935)
,,	Montana, U.S.A.	Hitchcock (1935)
6/1/2/6/2	California, U.S.A.	Sampson, Chase, and Hedrich (1951)
,,	Volga-Don, U.S.S.R.	Komarov (1934)

TABLE 4 (*Continued*)

Agrostological Index (Ag/An/E/F/P)	Locality	Literature Reference
6/1/2/7/2	Middle Dnieper, U.S.S.R.	Komarov (1934)
,,	Ciscaucasia, U.S.S.R.	Komarov (1934)
6/3/3/3/2	Arizona, U.S.A.	Hitchcock (1935)
,,	New Mexico, U.S.A.	Hitchcock (1935)
6/4/3/2/3	Coahuila and eastern Chihuahua, Mexico	Johnston (1943)
,,	Trans-Pecos region, Texas, U.S.A.	Cory and Parks (1937)
7/1/1/6/1	Patagonia	MacLoskie (1903-14)
,,	Wyoming, U.S.A.	Hitchcock (1935)
,,	Angara-Sayan, U.S.S.R.	Komarov (1934)
9/0/1/7/1	Karelian Lapland, U.S.S.R.	Komarov (1934)
,,	Dvina-Pechora, U.S.S.R.	Komarov (1934)
,,	Ob, U.S.S.R.	Komarov (1934)

indices identical with those derived from overseas floras. However, in several instances the Australian index differs from one or more overseas indices in only one unit, indicating a close similarity in the tribal composition of the grass flora. This is shown in Table 5.

The following Australian localities have no close overseas analogues among those surveyed:

(i) Darling, N.S.W. (Turner 1903*b*).
(ii) Western Plains, N.S.W. (Turner 1905).
(iii) North-eastern Victoria (Field Naturalists' Club of Victoria 1928).
(iv) Southern Victoria (Field Naturalists' Club of Victoria 1928).
(v) Murray Lands, South Australia (Black 1943).
(vi) Far north, South Australia (Black 1943).
(vii) South-western Queensland (Hartley, unpublished data).
(viii) De Grey region, W.A. (Burbidge, unpublished data).

The age and unreliability of much of the Australian floristic data must be borne in mind in interpreting this table, as well as the fact that the taxonomic affinities of some of the larger Australian grass genera are still uncertain. When allowance is made for these factors, it appears that similarities in the agrostological indices of Australian and overseas localities agree fairly well with similarities in plant environment as judged by climatic and other data. The similarity in the tribal composition of the grass flora of the Adelaide region and the State of Minnesota is, however, anomalous, and is not in accordance with climatic comparisons.

Most of the floras hitherto discussed have covered large areas, each with a great diversity of topography, soil, and even climate. It is of some interest to consider whether the agrostological index gives useful and consistent results when used for smaller areas in which the reliability of the floristic data compensates in a measure for the smaller number of species.

TABLE 5

AUSTRALIAN AND OVERSEAS LOCALITIES WITH SIMILAR AGROSTOLOGICAL INDICES

Locality	Agrostological Index (Ag/An/E/F/P)	Literature Reference
New England, N.S.W.	4/3/3/3/5	Turner (1903*a*)
Kentucky, U.S.A.	4/3/3/4/5	Hitchcock (1935)
Maryland, U.S.A.	4/3/3/4/5	Hitchcock (1935)
Missouri, U.S.A.	5/3/3/3/5	Hitchcock (1935)
South-western N.S.W.	2/3/4/3/4	Turner (1904)
George, Knysna, Humansdorp, and Uniondale, South Africa	2/3/4/3/3	Fourcade (1941)
Uitenhage and Port Elizabeth, South Africa	2/3/3/3/4	Schonland (1919)
Buenos Aires, Argentina	2/3/3/3/4	Parodi (1946)
North-western Vic.	4/2/3/4/4	Field Naturalists Club of Victoria (1928)
Illinois, U.S.A.	5/2/3/4/4	Hitchcock (1935)
New York, U.S.A.	5/2/3/4/4	Hitchcock (1935)
West Virginia, U.S.A.	5/2/3/4/4	Hitchcock (1935)
South-western Vic.	6/1/1/5/3	Field Naturalists Club of Victoria (1928)
North I., N.Z.	7/1/1/5/3	Cheeseman (1906), Allan (1940)
Eastern Vic.	5/1/2/5/4	Field Naturalists Club of Victoria (1928)
Wisconsin, U.S.A.	5/1/2/4/4	Hitchcock (1935)
Minnesota, U.S.A.	5/1/2/5/3	Hitchcock (1935)
Michigan, U.S.A.	6/1/2/5/4	Hitchcock (1935)
Cayuga Quadrangle, New York, U.S.A.	5/1/2/6/4	Clausen (1949)
South-eastern S.A.	5/1/1/5/3	Black (1943)
Minnesota, U.S.A.	5/1/2/5/3	Hitchcock (1935)
Southern S.A.	4/1/1/5/2	Black (1943)
Valencia, Spain	4/2/1/5/2	Carbonell (1950)
San Diego Co., California, U.S.A.	4/1/2/5/2	Higgins (1949)
Syr Darya foothills, U.S.S.R.	4/1/2/5/2	Komarov (1934)
Mountain Turkmenia, U.S.S.R.	4/1/1/6/2	Komarov (1934)
Kimberley District, W.A.	0/6/4/0/6	Gardner (unpublished data)
Western Vega Real valley, Santa Domingo	0/6/4/1/6	Morosco (1943)

Australian floristic information is not readily available for such a study, but suitable data for Great Britain is given in The Comital Flora of the British Isles (Druce 1932). This gives the distribution of grasses and other plants for each of the 112 vice-counties into which Great Britain is divided. These vice-counties range in size from the Isle of Wight, of 147 sq. miles, to eastern and western Inverness, each of more than 2000 sq. miles. The boundaries of the vice-counties are related to those of administrative units rather than to natural regions, and hence the larger vice-counties still include various types of topography and soil. Nevertheless the restrictions of total area impose some limitations on these variations.

TABLE 6

AGROSTOLOGICAL INDICES OF BRITISH VICE-COUNTIES

Agrostological Index	Vice-counties*	Distribution By Countries		
		England	Wales	Scotland
4/0/0/8/0	95			X
4/0/0/8/1	79			X
4/0/0/9/0	81/87/99			X
4/0/0/9/1	83			X
5/0/0/8/0	100/102/104/107/108/111/112			X
5/0/0/8/1	6/15/16/33/49/51/53/60/67/80	X	X	X
5/0/0/9/0	8/36/42/43/44/45/47/48/57/65/72/73/74/75/76/77/84/88/89/93/94/97/101/105/106	X	X	X
5/0/0/9/1	7/17/21/23/24/32/34/35/39/52/55/56/63/64/66/70/78/92	X	X	X
6/0/0/8/0	46/71/91/96/103/109/110		X	X
6/0/0/8/1	1/3/9/10/11/13/19/20/25/29/ 30/54/58/59/61/62	X		
6/0/0/9/0	5/31/40/50/68/69/82/85/98	X	X	X
6/0/0/9/1	2/4/12/14/22/37/38/86/90	X		X
7/0/0/8/1	18/26/27/28/41	X	X	

* For a key to these vice-counties see Druce (1932).

The number of grass species recorded from the vice-counties ranges from 103 for South Hampshire down to 42 for the Outer Hebrides. About 23 grass species are recorded for every vice-county, while some others have a very restricted distribution, being confined to one or two vice-counties. Throughout Great Britain species of Agrosteae and Festuceae are predominant among the grasses, and the whole country, as well as each vice-county, falls within the Ag/F iso-agrostological zone. This is in accordance with expectations, for the mean midwinter (January) temperature throughout is below 50°F, which has been shown to be significant for grass distribution (Hartley 1950). The tribes Andropogoneae and Eragrosteae are completely absent from the British flora.

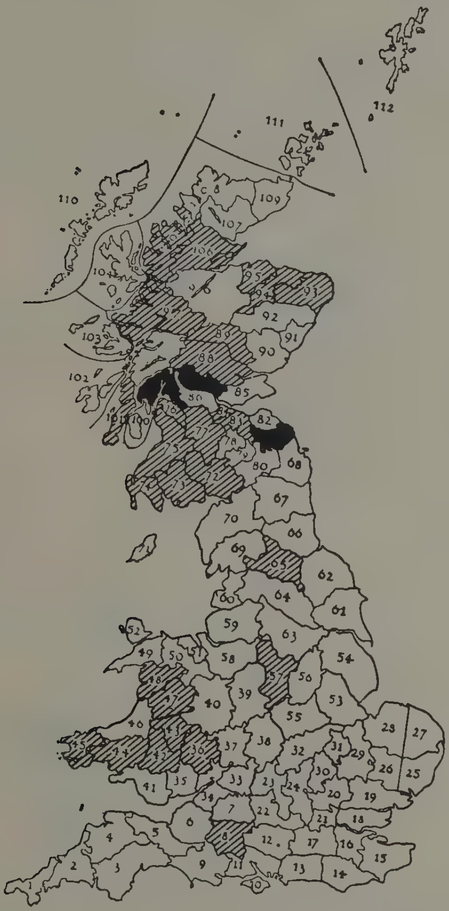

112
111
110
109
108
107
106
105
104
103
102
101
100
96
95
94
93
92
91
90
89
88
86
85
83
82
81
80
79
78
77
75
73
72
70
69
68
67
66
65
64
63
62
61
60
59
58
57
56
55
54
53
52
50
49
48
47
46
45
44
43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1

Fig. 2.—Vice-counties of the United Kingdom. Solid black, agrostological index 4/0/0/9/0. Hatched, indices differing by one unit from 4/0/0/9/0.

Thirteen agrostological indices are represented in the vice-comital flora of Great Britain, and their distribution is given in Table 6.

From this table it is apparent that while the more frequent indices occur in vice-counties in each of the three countries, there is a general trend from those with a low proportion of Agrosteae, which are confined to Scotland, to those which have a high proportion of this tribe and occur principally or exclusively in England and Wales. The indices for the other tribes are less significant, as the total range of variation covered is smaller.

Figures 2 and 3 show the distribution of the vice-counties with the most contrasting indices, viz. 4/0/0/9/0 and 7/0/0/8/1. Areas with indices differing by only one unit from these are also shown on the maps. The index 4/0/0/9/0 occurs in central and southern Scotland, while related indices occur in other parts of Scotland and in the mountainous areas of Wales and the Pennines. The occurrence of a related index in vice-county 8 (South Wiltshire) appears to be anomalous. Generally, all these areas are characterized by high elevation, high rainfall, and low temperatures.

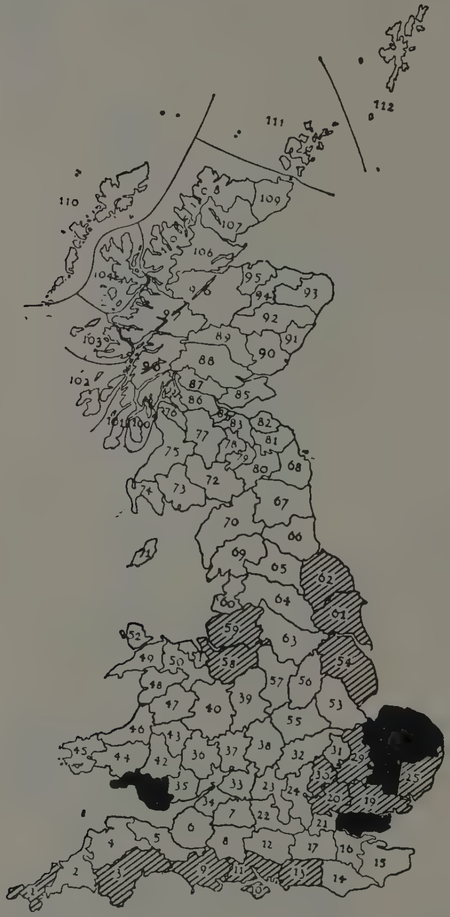


Fig. 3.—Vice-counties of the United Kingdom. Solid black; agrostological index 7/0/0/8/1. Hatched, indices differing by one unit from 7/0/0/8/1.

These environmental factors are so closely associated throughout Great Britain that it is not possible to assess separately their significance for grass distribution.

By contrast, the index 7/0/0/8/1 occurs principally in East Anglia, with similar indices along the south and east coast of England and in the Cheshire Plain. It is also found, perhaps anomalously, in Glamorgan. These areas are typically low-lying, dry, and warm.

There is thus a general agreement between grass distribution, as indicated by the agrostological indices, and the major climatic factors, although the exceptions are sufficiently numerous to suggest that the indices should be applied with caution to restricted areas. On the other hand there is little or no correlation between the agrostological indices and the distribution of such edaphically determined vegetation types as the Chalk Downs. The relationship between the agrostological index and the plant environment is only evident when the area covered is sufficiently large and diversified to include a range of edaphic types which enable the flora to develop to the full extent permitted by the climate.

V. General Discussion

The studies reported in this paper show that the pattern of grass distribution throughout the world exhibits considerable regularity and a general agreement with the distribution of temperature and other climatic factors. The regularity of the pattern shown is indeed remarkable, as the data used have been derived from the published studies of many authors working independently in widely separated countries since the beginning of the present century. As the agrostological index used is essentially an index of *comparative* specific diversification, it would not necessarily be altered by changing concepts of specific delimitation, provided that these did not produce differential results between the tribes. Thus a "lumper" might recognize only 100 grass species for any locality while a "splitter" recognized 200 or more. This would not affect the index unless the splitter changed the proportions of species of each tribe present, for instance by tripling the number of species of Eragrosteae while leaving those of Festuceae unchanged. The infrequency of apparent anomalies in the index suggests that such differential splitting has occurred only rarely.

The regularity of the pattern also has implications in relation to evolutionary changes. A rapid rate of species formation in some tribes in some regions, unmatched by paralled developments in the same tribes elsewhere, would destroy any general concordance of the agrostological index with the distribution of climatic factors, unless there was a general tendency for new species to replace related pre-existent ones, or unless the rate of spread of species into climatically suitable areas was great in comparison with their rate of formation. The limited genetic evidence available does not indicate any tendency for uniform rates of species formation in different plant groups and in different regions, or for the general replacement of pre-existent species by new ones. Thus it appears that the rate of spread of new grass species throughout their potential range must generally be rapid in comparison with their rate of formation. Where the spread of species has been restricted by major geographical barriers — as in California, Hawaii, and possibly Australia — anomalous indices are found.

The agrostological index is a purely floristic one, being based entirely on the occurrence of species in a particular region, without weighting according to their relative abundance. As such, it has much in common with the life-form system of Raunkiaer, which, as pointed out by Dansereau (1951), is also essentially floristic, although the choice of the life forms used is based on their supposed ecological significance.

In a recent review, Cain (1950) has emphasized the general correspondence between life-form pattern and phytoclimate, although many exceptions are noted, and it is suggested that "climatic differences may be more sensitively reflected by spectra for associations than by spectra for the total flora of large areas." A similar viewpoint is expressed by Dansereau (1951), who comments "The surprising feature in Raunkiaer's life-form system is that it should show such close correlation with major climatic units — in spite of being essentially floristic, as generally applied by Raunkiaer, and not vegetational".

In the light of the evidence presented in this paper, this viewpoint appears to require some modification. The agrostological index is wholly floristic, and yet shows a correlation with climate at least comparable with that shown by Raunkiaer's life-form spectra. Indeed, it appears *a priori* improbable that vegetational indices should show a closer relationship to climate than suitably selected floristic indices. Most associations and smaller vegetational units have a distribution which is affected by edaphic and biotic influences as well as by climatic ones. These influences may greatly affect the relative abundance of different species, but they rarely affect the presence or absence of them, provided that the area selected is sufficiently large and diversified to include a wide range of soils and biotic influences. A floristic index may be expected to show a close correlation with climate provided that the area covered includes a diversity of habitats, and the floristic unit selected has a wide distribution which is not greatly affected by historical influences. The proposed agrostological index fulfils both these requirements in large measure, and may therefore be useful in studies of the distribution of pastures and pasture plants. It is not to be expected that it should be equally useful in distribution studies of plants of totally different growth habit, such as forest trees.

The value of the agrostological index as a practical guide in the problems of pasture plant introduction cannot be fully assessed from the data presented. Its usefulness is severely limited by the lack of published data on plant distribution in many regions, notably including Australia. Nevertheless, the indications are that it may be of value where adequate data are available. Thus from Table 5 it will be noted that the closest overseas parallels to the New England district of New South Wales are the States of Kentucky, Maryland, and Missouri, U.S.A. These States are all predominantly within the 1b pasture plant zone of the U.S.A. (Wheeler 1950), for which the recommended introduced pasture grasses are *Agrostis tenuis* Sibth., *Poa pratensis* L., *Bromus inermis* Leyss. (in part), *Festuca rubra commutata* Gaud., *Festuca elatior* L., *Festuca rubra* L., *Festuca arundinacea* Schreb., *Dactylis glomerata* L., *Agrostis alba* L., *Phalaris arundinacea* L., *Lolium multiflorum* Lam., *Lolium perenne* L., *Sorghum vulgare sudanense* (Piper) Hitchc., *Arrhenatherum elatius* (L.) Mert. and Koch, *Phleum pratense* L., *Zoysia japonica* Steud., and *Zoysia matrella* (L.) Merr.

During recent years many introduced pasture grasses have been tested by C.S.I.R.O. officers, both at the Chiswick Field Station, Armidale, and at other centres on the Northern Tablelands. Insofar as species in the above list have been included in the trials they have all been exceptionally promising, especially when the soil fertility has been built up to a level enabling them to develop to full advantage (E. J. Hilder, personal communication). Particularly noteworthy is the outstanding success of the Kentucky 31 strain of tall fescue which is quite characteristic of the American zone mentioned, and is one of the best of the grasses under trial at Armidale.

While such an example is not conclusive it encourages the belief that the performance of pasture plants in any one locality affords a useful guide to their potentialities in another locality of comparable agrostological index, provided that the index is based on a full knowledge of the flora and that the relationships of the genera concerned are fully understood.

VI. References

ABOLIN, R. (1935).—"Plant Resources of Turkmenistan." p. 290 (In Russian). (Institute of Plant Industry: Leningrad.)

ALLAN, H. H. (1940).—Handbook of the naturalized flora of New Zealand. Dep. Sci. Industr. Res. N.Z. Bull. No. 83.

ATLAS OF AMERICAN AGRICULTURE (1936).—(U.S. Dep. Agric.: Washington, D.C.)

BEADLE, N. C. W. (1948).—Vegetation of western New South Wales. Doctoral Thesis: University of Sydney.

BEETLE, A. A. (1947).—Distribution of the native grasses of California. *Hilgardia* **17** (9): 309-57.

BLACK, J. M. (1943).—"Flora of South Australia." Part 1. 2nd. Ed p. 253. (Govt. Printer: Adelaide.)

BRIQUET, J. (1910).—"Prodrome de la Flore Corse." Vol. 1, p. 656. (Georg. et Cie: Lyon.)

CAIN, S. A. (1950).—Life-forms and phytoclimate. *Bot. Rev.* **16** (1): 1-32.

CAMPBELL, D. H., and WIGGINS, I. L. (1947).—Origins of the flora of California. *Stanford Univ. Publ. Biol. Sci.* **10** (1).

CARBONELL, J. B. (1950).—Estudio fitografico de la Sierra de Corbera. *Ann. Jard. Bot. Madrid* 9: 361-484.

CHEESEMAN, T. F. (1906).—"Manual of the New Zealand Flora." 2nd Ed. p. 1163. (Wellington.)

CLAUSEN, R. T. (1949).—Check-list of the vascular plants of the Cayuga quadrangle. Cornell Univ. Agric. Exp. Sta. Mem. No. 291.

CORY, V. L., and PARKS, H. B. (1937).—Catalogue of the flora of the State of Texas. Texas Agric. Exp. Sta. Bull. No. 550.

DANSEREAU, P. (1951).—Description and recording of vegetation upon a structural basis. *Ecology* 32 (2): 172-229.

DRUCE, G. C. (1932).—"The Comital Flora of the British Isles." p. 407. (T. Buncle & Co.: Arbroath.)

FOURCADE, H. G. (1941).—Check-list of flowering plants of George, Knysna, Humansdorp and Uniondale. Bot. Surv. S. Afr. Mem. No. 20.

FIELD NATURALISTS CLUB OF VICTORIA (1928).—"A Census of the Plants of Victoria." 2nd Ed. p. 93. (Melbourne.)

HALACSY, E. DE (1900-08).—"Conspectus Florae Graecae." 3 Vols. and suppl. (Leipzig.)

HARTLEY, W. (1950).—The global distribution of tribes of the Gramineae in relation to historical and environmental factors. *Aust. J. Agric. Res.* 1 (4): 355-73.

HIGGINS, E. B. (1949).—Annotated distributional list of the ferns and flowering plants of San Diego County, California. Occas. Pap. San Diego Soc. Nat. Hist. No. 8.

HITCHCOCK, A. S. (1927).—Grasses of Ecuador, Peru and Bolivia. *Contr. U.S. Nat. Herb.* 24 (8): 291-556.

HITCHCOCK, A. S. (1935).—"Manual of the Grasses of the United States." p. 1040. (United States Government Printing Office: Washington.)

HITCHCOCK, A. S. (1936).—Manual of the grasses of the West Indies. Misc. Publ. U.S. Dep. Agric. No. 243.

HUBBARD, C. E., and VAUGHAN, R. E. (1940).—"The Grasses of Mauritius and Rodriguez." p. 128. (Crown Agents for the Colonies: London.)

JOHNSTON, I. M. (1943).—Plants of Coahuila, eastern Chihuahua, and adjoining Zacatecas and Durango, II. *J. Arnold Arbor.* 24 (4): 375-421.

KAWAKAMI, T. (1910).—"A List of Plants of Formosa." p. 119. (Japanese and English.) (Taihoku.)

KNOCKE, H. (1921-23).—"Flora Balearica." Vols. 1-4. (Montpellier.)

KOMAROV, V. L. (1934).—"Flora U.R.S.S." (Acad. Sci. U.R.S.S.: Moscow.)

KOORDERS, S. H. (1911).—"Exkursionflora von Java." Bd. 1 (Jena.)

KOPPEN, W. (1923).—"Die Klimate der Erde." (Walter de Gruyt: Berlin.)

MACBRIDE, J. F. (1936).—Flora of Peru, part 1. Field Mus. Nat. Hist. Publ. No. 351.

MACLOSKIE, G., ET AL. (1903-14).—Reports of the Princeton University expeditions to Patagonia, 1896-99, Vol. 8.

MOROSCO, R. M. (1943).—"Catalogus Florae Domingensis." p. 732. (New York.)

NUTTONSON, M. Y. (1950).—Agricultural climatology of Siberia. Amer. Inst. Crop Ecol. Study No. 13.

PARODI, L. R. (1946).—"Gramineas Bonariensis." 4th Ed. p. 112. (Acme Agency: Buenos Aires.)

PITARD, J., and PROUST, L. (1908).—"Les Iles Canaries, Flore de l'Archipel." (Paris.)

RAGONESE, A. E. (1941).—La vegetacion de la provincia de Santa Fe. *Darwiniana* 5: 369-416.

RAUNKIAER, C. (1934).—"The Life Forms of Plants and Statistical Plant Geography, being the collected papers of C. Raunkiaer." p. 632. (Clarendon Press: Oxford.)

RIDLEY, H. N. (1922).—"Flora of the Malay Peninsula." 5 Vols. (L. Reeve and Co. London.)

RODWAY, L. (1903).—"Flora of Tasmania." p. 320. (Govt. Printer: Hobart.)

SAMPSON, A. W., CHASE, A., and HEDRICK, D. W. (1951).—California grasslands and range forage grasses. Calif. Agric. Exp. Sta. Bull. No. 724.

SCHONLAND, S. (1919).—Phanerogamic flora of Uitenhage and Port Elizabeth. Bot. Surv. S. Afr. Mem. No. 1.

SHANTZ, H. L., and ZON, R. (1924).—Natural vegetation of the United States, *in* Atlas of American Agriculture. (U.S. Department of Agriculture: Washington.)

STANDLEY, P. C., and RECORD, S. J. (1936).—The forests and flora of British Honduras. Field Mus. Nat. Hist. Publ. No. 350: 432.

THORNTHWAITE, C. W. (1931).—The climates of North America according to a new classification. *Geogr. Rev.* 21: 633-55.

TURNER, F. (1903*a*).—The vegetation of New England, N.S.W. *Proc. Linn. Soc. N.S.W.* **28**: 276-311.

TURNER, F. (1903*b*).—The botany of the Darling, N.S.W. *Proc. Linn. Soc. N.S.W.* **28**: 406-42.

TURNER, F. (1904).—The botany of south-western New South Wales. *Proc. Linn. Soc. N.S.W.* **29**: 132-81.

TURNER, F. (1905).—The botany of north-western New South Wales. *Proc. Linn. Soc. N.S.W.* **30**: 32-90.

WHEELER, W. A. (1905).—"Forage and Pasture Crops." p. 752. (D. van Nostrand Co.: New York.)

WILLIS, J. C. (1911).—"A Revised Catalogue of the Indigenous Flowering Plants and Ferns of Ceylon." (Colombo.)

RADIAL FISSURES IN THE EARLY WOOD OF CONIFERS

By G. L. Amos*

(*Manuscript received June 4, 1953*)

Summary

In certain conifers anatomical evidence suggests that young trees may become exposed to conditions conducive to collapse during late wood formation, causing partial collapse and radial cleavages in the early wood. Living ray cells are exposed to the cavity after cleavage. Different species show different responses conditioned by the anatomy and physiology of the ray parenchyma. The cavities fill with cellular tissue in radiata pine (*Pinus radiata* D. Don), with resin in Douglas fir (*Pseudotsuga taxifolia* (Poir.) Britt.), and remain empty in white spruce (*Picea glauca* (Moench) Voss).

Evidence is presented to show that when a living protoplast is given free access to moist air, a powerful growth stimulus is applied to the cell. In radiata pine, ray parenchyma cells have primary walls only, and the response is a proliferation of these cells. In Douglas fir and white spruce, the ray parenchyma has secondary thickening and small ray tracheid pitting, precluding growth. The response is an increased metabolic rate, producing resin in Douglas fir (heartwood-forming species) and without solid end-products in white spruce (species with little contrast between sapwood and heartwood).

I. Introduction

Various observers have commented on drought and frost cracking in standing conifers where the injury has been evident superficially, and Day (1950), reviewing these defects, made a brief reference to internal checking in spruce. Pryor (1947) was the first to make a survey of the occurrence of internal checking in radiata pine (*Pinus radiata* D. Don), and he recorded its sporadic occurrence over a wide area of south-eastern Australia. The fissures were elliptical or lenticular in cross section, varying from 1/32 to 3/16 in. wide, and extending up to several feet in length following the grain spiral. In radial extent he found that they invariably started at the extreme outer edge of the 'autumn' wood and finished within the growth ring after 'autumn' wood again started to form. They were filled with soft tissue, were most common in young stems less than 6 in. in diameter, and more common near the butt than higher up the stem. Pryor attributed the defect to the effect of frost, because his field work suggested that thin bark, absence of closed canopy, and proximity to the ground favoured the cause of this type of damage, and such conditions were consistent with frost injury. He also advanced the explanation, from superficial examination only, that frosts or temperature fluctuation during dormancy ruptured the cambium sheet, forming a gap which persisted during spring growth and closed up during 'autumn' wood formation later in the same growth season.

---

* Division of Forest Products, C.S.I.R.O.; present address: Commonwealth Research Station, Merbein, Vic.

Reid and Mitchell (1951) made a study of the phenomenon in New Zealand Douglas fir (*Pseudotsuga taxifolia* (Poir.) Britt.). The checks were spindle- or diamond-shaped in cross section, often over 6 in. long, confined to the early wood zones in growth rings with a high percentage of early wood, and did not extend beyond a single growth ring. They were generally filled with a viscous "gum". Reid and Mitchell attributed the checks to drought, but were unable to find a correlation between the frequency of checking and climatic conditions at the time the surrounding early wood tracheids were being laid down.

A more fundamental approach was made by Lutz (1952), who observed internal radial checking in Alaskan white spruce (*Picea glauca* (Moench) Voss). The clefts were diamond-shaped, 6-8 in. long, confined to the wider growth rings with a relatively large proportion of early wood, and did not extend beyond the growth ring in which they occurred. They were characterized by absence of filling, the late wood was drawn inwards at the point of injury, and a band of traumatic tissue extended outwards from the point of injury. Lutz concluded that the clefts were formed during the dormant season because absorption of water was prevented by the frozen ground inhibiting replacement of transpiration loss and causing the thinner-walled early wood tracheids to collapse.

II. THE DEFECT IN PINUS RADIATA

(*a*) *Characteristics*

A further study of the defect in *Pinus radiata* has been made because of trouble encountered in peeling of veneers (Plate 1, Fig. 1) from affected logs (Plate 1, Fig. 2). As in Alaskan white spruce and New Zealand Douglas fir, the affected areas in *Pinus radiata* occurred in the early wood. In addition to the characteristics of the fissures reported by Pryor, there were several others. Along the edges of each fissure, the wood was light brown, intermediate in colour between the normal wood and the darker filling. Secondly, the inner edge did not always immediately follow a late wood band as reported by Pryor. Many of the fissures shown in Plate 1, Figure 2, do not extend inwards so far, and by following several of them up and down the bole, it was shown that some of them did not reach the previous late wood band at any point.

The log illustrated in Plate 1, Figure 2, was obtained from the Penola forest in South Australia, and the author has examined material in the field in the Australian Capital Territory. In any one locality, the more severe effects are observed in the growth rings of specific years, and then in the wider growth rings at particular levels (Table 1). Thus, in the Australian Capital Territory, trees were examined in which severe effects were produced in two growth rings 3 yr apart. Only the first of these was evident at the butt, but at 10 ft the second ring was the most severely affected. At this level, the second ring was much wider than it was at the butt, with a much more extensive early wood. Occasional fissuring was observed at a height of 30 ft, but in general, severe effects were confined to levels below 20 ft.

South Australian forest officers associate the condition with an environment adjoining temporary swamps, where the soil is almost saturated for several months in some years. On the basis of field work, mostly in the Australian Capital Territory, other workers, e.g. Pryor (1947), favour an association with cold or frost. From Table 1 it may be observed that more frosts occurred during the years of most severe fissuring in South Australia than in other years, suggesting a possible correlation. However, not all trees in a frost hollow are affected, even in the Australian Capital Territory forests, and consideration of the factors involved will be presented later in this paper.

TABLE 1
RELATION BETWEEN OCCURRENCE OF DEFECT, RING WIDTH, AND FROSTS
Log from Penola, S.A.

Year	Ring Thickness (in.)	No. of Checks in Cross Section	No. of Frosts in First-named Year
1942-43	0.40	Nil	25
1943-44	0.35	1	25
1944-45	0.45	6	38
1945-46	0.51	32	56
1946-47	0.41	48	55
1947-48	0.26	3	21
1948-49	0.21	Nil	22
1949-50	0.14	1	46
1950-51	0.25	1	27

Lutz (1952) and Reid and Mitchell (1951) gave some weight to the weak development of the late wood in the years of most severe cracking, but in *P. radiata* reference to Plate 1, Figure 2, shows that the development of the late wood is more extensive in rings which have checked than in subsequent rings. A weakly developed late wood therefore had no direct bearing on the occurrence of checking, and in white spruce and Douglas fir may have reflected the adversity of the growth conditions in the latter part of the growing season. The significance of this feature escaped Reid and Mitchell but was fully appreciated by Lutz.

Differences between the fissures in white spruce, Douglas fir, and radiata pine were found in the nature of the filling. In white spruce the clefts were empty, in Douglas fir they were filled with a clear, semi-liquid resin, and in *P. radiata* they were filled with cellular tissue (Plate 1, Fig. 8) without any apparent organization. In radiata pine there was no band of traumatic tissue extending into the next growth ring such as was found in white spruce.

(*b*) *Time of Checking*

A typical abnormality in radiata pine is shown in Plate 1, Figure 8, but the essential features are more clearly illustrated in Figure 1. Here six radial series of tracheids between which a fissure has developed are shown.

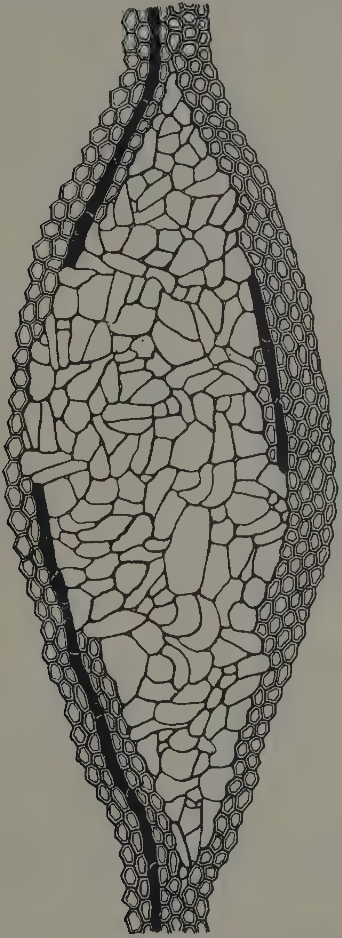


Fig. 1.—Radial check in *Pinus radiata* filled with abnormal tissue. Note that the ray or tracheid files appear on one side of the abnormal tissue in positions corresponding to their absence on the other.

The radial series of tracheids which are not continuous and the ray appear alternately along one border of the fissure or the other, their presence on one side corresponding to their absence on the other. There is no doubt that when these cells were first laid down, all series were continuous and adjacent to one another. Although the general direction of cleavage is radial, groups of cells have been torn out of their files during splitting, and taken to the opposite side of the fissure.

The anatomy of the abnormality therefore establishes that cleavage in the early wood must have occurred during subsequent late wood formation and the filling of the space with cellular tissue after checking, probably during the next growing season. The suggestion of Pryor (1947) that a rupture occurs in the cambium sheet during the early part of the growing season, and subsequently closes up, is therefore untenable. Cleavage could not have reached the cambium because there is no band of traumatic tissue extending beyond the limit of the injury. This differs from the cleavage in white spruce, which extends from the first-formed early wood to the cambium (Lutz 1952).

It is now apparent why Reid and Mitchell (1951) found no correlation between the occurrence of checks and climatic conditions during the early part of the growing season, because causative agents must be sought in the later part of the growth year while the tree is forming late wood. Again, in white spruce, the severity of the damage — tearing away of the early wood from the previous late wood, and traumatic tissue extending beyond the cleft — is possibly attributable to the more severe conditions imposed by the Alaskan winter compared with New Zealand and Australia.

(*c*) *Cause of Cleavage*

From the examination of Reid and Mitchell's material, investigators at the U.S. Forest Products Laboratory, Madison, Wisconsin, attributed the phenomenon to collapse of the thin-walled early wood fibres. Lutz showed that the clefts in white spruce were laterally adjoined by areas of collapsed early wood. The same feature is apparent in *P. radiata* (Plate 1, Figs. 3 and 4), the tracheids between the areas of abnormal tissue being in a state of partial collapse.

(*d*) *Response to Cleavage in* P. radiata

The mechanism of abnormal tissue formation in *P. radiata* has been studied by serial tangential sections of a recently formed fissure. All groups of cells within the cavity were in contact with a ray, the intervening spaces between groups being empty. There seems to be no doubt that the ray cells exposed to the cavity during cleavage are the sole source of the cellular mass filling the older fissures as shown in Plate 1, Figure 8.

The rays in *P. radiata* contain two anatomically distinct elements, firstly ray tracheids with dentate thickening and bordered pits between them and the adjoining tracheids (Plate 1, Fig. 6), and secondly ray parenchyma with thin, delicate walls (Plate 1, Fig. 5) and large simple pits connecting with tracheids (Plate 1, Fig. 7). If the tracheid wall is pulled away from the ray (Plate 2, Fig. 1) these thin-walled cells remain intact. Examination of their walls, using plane-polarized light and crossed nicols, shows a very weak birefringence characteristic of primary walls (Plate 2, Fig. 2). Plate 2, Figures 1 and 2, represents the same ray for comparison, and shows clearly the wall differences between these cells and the thickened ray tracheids.

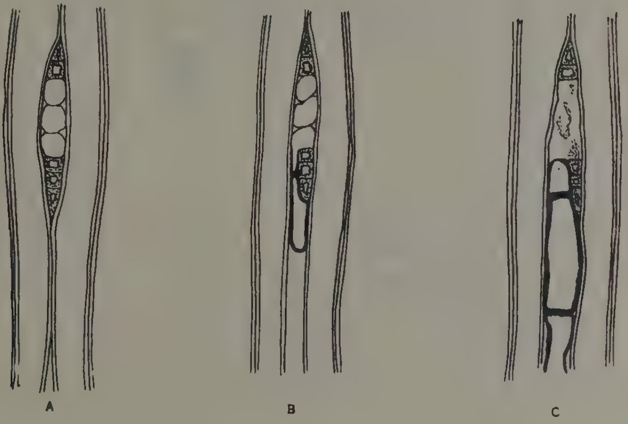


Fig. 2.—Ray of *Pinus radiata* in tangential section. *A*, in normal wood, showing three series of thin-walled parenchyma cells and upper and lower bi- and triseriate groups respectively of thickened ray tracheids. *B*, at radial margin of cleavage. The ray parenchyma proliferating into the fissure. *C*, further in the fissure. Proliferated parenchyma and persistent ray tracheids.

The series of changes in such a ray was followed through unaffected wood into the zone of cleavage, three stages being shown in Figure 2. In sections cut short of the affected area, the ray contained three series of ray parenchyma elements between upper and lower bi- and triseriate groups of ray tracheids (Fig. 2*A*). At the radial limit of cleavage, a stage shown in Figure 2*B* was observed. The parenchyma cell nearest the cavity had grown out past the lower series of ray tracheids and divided. Deeper in the affected area (Fig. 3*C*) further proliferation of these cells was observed, a photograph of such a stage being shown in Plate 2, Figure 6.

The ray itself may be ruptured by the cleavage as shown in Figures 3*A* and 3*B*. Thus, Figure 3*A* shows a ray with four groups of ray tracheids. In the affected zone three of these persisted along one lateral margin of the fissure whereas the biseriate group nearest the centre was found along the opposite side, the intervening space being filled with cellular tissue from the proliferated ray parenchyma. A photomicrograph of a stage similar to Figure 3*B* is shown in Plate 2, Figure 5.

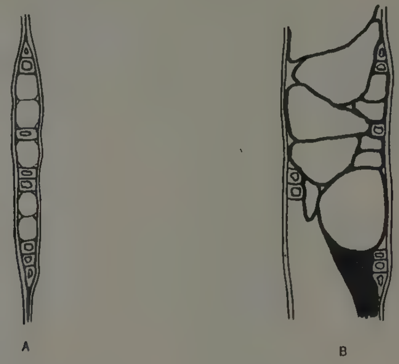


Fig. 3.—Ray of *Pinus radiata* in tangential section. *A*.—In normal wood, showing four and three groups respectively of ray tracheids and ray parenchyma. *B*.—In the affected area, showing proliferated ray parenchyma, and one group of ray tracheids adherent to the opposite side of the fissure.

III. DISCUSSION

There can be little doubt that the defects considered above in white spruce, Douglas fir, and radiata pine are produced by essentially similar causative agents late in the growing season.

Mention has been made of some of the possible causative agents, the factors to be considered including:

(*a*) Stress pattern in the tree,
(*b*) Effects of cold,
(*c*) Effects of saturated soil,
(*d*) Width of the rings,
(*e*) Structure of the wood, and
(*f*) Anatomy of the defect.

Jacobs (1946) has presented convincing evidence that the normal stress pattern in the outer ring of a growing tree is that of longitudinal tension, circumferential compression, and radial tension. Whatever the condition causing cleavage, it must produce a local change from circumferential (tangential) compression to tension, and then only in the outer ring. The maximum effect is also produced at some distance in from the cambium.

The tendency for the etiology of the defect to be associated with cold conditions suggests that cold may have either a direct or indirect effect in producing fissures. The coefficients of expansion for green *P. radiata* wood have been determined, and differ according to the direction of measurement:

Tangential (circumferential)	Negative	Very small
Radial	Positive	7×10^{-6}
Longitudinal	Negative	Negligible

Because the circumferential coefficient of expansion is negative, the question of contraction of the tissues causing fissuring does not arise, and a direct effect of cold on the wood substance is therefore eliminated. However, fissuring occurs in the sapwood of the trees at a time when the whole cross section of the trees is sapwood. It is therefore possible that the expansion of the wood with decreasing temperature combined with the contraction of the contained sap would produce conditions conducive to partial collapse of the tracheids. The cambium zone and differentiating sapwood would be sufficiently plastic to accommodate itself to these dimensional changes, whereas the differentiated and thickened tracheids further in from the cambium would be subjected to more intense stresses. If this were so, it would explain the limited radial extent of individual fissures, the association with cold conditions, and the absence of fissures from later rings when heartwood development would create a reservoir, or expansion chamber, yielding up fluids to, or taking them from the sapwood when subjected to dimensional changes. It would also explain why, in the outer fissured rings as described for trees in the Australian Capital Territory, the fissures do not appear at the butt but appear at higher levels in the tree. At the butt, some heartwood would have been formed at the time of fissuring, whereas at higher levels the cross section would be entirely sapwood.

Kramer (1951) and others have shown that flooded soil reduces water uptake to such an extent that the rate of transpiration is reduced far below normal. In such circumstances a state of physiological unbalance in the water economy of the tree occurs so that water loss by transpiration cannot be balanced by uptake, and conditions conducive to collapse of the large early wood tracheids are produced. It is interesting that Reid and Mitchell attributed the effect in New Zealand Douglas fir to actual drought to which the areas were periodically subject. In Alaskan white spruce, the frozen ground would reduce water uptake whereas transpiration would not be directly affected. In this latter species, both the effects of cold discussed above and the physiological drought may have had a cumulative effect and produced more severe fissuring than in the other two species.

The effect was more severe in the wider growth rings (Table 1), i.e. rings with a wide band of relatively thin-walled early wood cells. The rings nearer to the centre of the tree are usually the widest in *P. radiata* and fissuring was most common in stems below 6 in. in diameter. Conditions conducive to collapse would produce effects primarily in such regions where the structure of the wood lends itself most readily to collapse effects.

Whatever the causative agent or agents may be, the anatomy of the defect leaves no doubt that fissuring was produced ultimately as a result of collapse of the early wood tracheids, at a time subsequent to their formation, i.e. in the late part of the growth season. The above discussion shows that correlations with cold and with water unbalance are both consistent with the anatomical observations in that either could produce a tension inside the conducting elements followed by partial collapse of the thin-walled early wood cells and cleavage along roughly radial planes in the early wood.

After cleavage, events in the three species are different. In white spruce, the cavity remains empty, in Douglas fir it becomes filled with resin, and in radiata pine there is a proliferation of cellular tissue. The key to these variations in response is to be found in the anatomy and physiology of the ray cells. It has been shown how the ray parenchyma of radiata pine, bounded only by primary wall, proliferates into the cavities. The structure of the walls is that of meristematic cells, and in circumstances where growth is unrestricted, such as occurs after cleavage, the cells behave as meristematic cells, growing and dividing. The primary wall, as in all growing cells, is capable of great extension.

In white spruce and Douglas fir, the situation is different. The ray parenchyma becomes thickened with secondary wall often more than the ray tracheids (Plate 2, Figs. 3 and 4). The pitting to the tracheary elements is simple but small (Plate 2, Figs. 7 and 8). The thickened cell walls preclude proliferation of the type found in radiata pine, because they are not capable of extension. Gerry (1914) observed that, in conifers, tylosis formation is dependent on the size of the pits between medullary ray cells and tracheids, only those with large ray pits forming them. The small pit sizes in white spruce and Douglas fir therefore preclude tylosis formation as a means of filling the cavity. Anatomical considerations thus account for the differences in response of radiata pine on the one hand and Douglas fir and white spruce on the other.

It still remains to be shown why the clefts in white spruce are empty and those in Douglas fir become filled with resin. Although Chattaway (1949) worked only with hardwoods, some of her observations on the different behaviour of rays during sapwood-heartwood transition are of interest in this discussion. She found that Gerry's observation on the relation between pit size and tylosis formation applied during heartwood formation, only woods with large vessel-ray pitting forming tyloses. However in a number of species with small pits, she found that a copious secretion of "gum" into the vessel lumen occurred, and concluded that both tylosis formation and resin secretion were different responses to the same growth stimulus, the factor determining the type of response being the pit size. Chattaway was only concerned with species which formed a definite heartwood, and did not give any consideration to the so-called "sapwood trees" or trees with an "indistinct" heartwood. If the findings of Chattaway are applicable to conifers, there is every reason to expect that the cavities in Douglas fir should fill with resin rather than with cellular outgrowths because of the small pit size in the walls of the ray parenchyma cells exposed to the cavity after cleavage.

Whereas Douglas fir forms a distinct heartwood, in white spruce there is little contrast between sapwood and heartwood. That is, the burst of activity of the ray cells before their death in Douglas fir produces resinous or coloured materials as an end-product, whereas in white spruce this is not so. The empty cavities in white spruce are therefore attributable to a biochemical variant in the metabolism of the ray cells, such as is commonly found between species.

This argument presents the response to cleavage in the three species as variants in the response to a growth stimulus, determined by the anatomy and physiology of the ray parenchyma, but it has been assumed that cleavage of the early wood fibres exposing living ray cells to an air pocket provides a stimulus for growth, and parallels between these conditions and those existing during tylosis formation in other species have been freely drawn. It remains to justify both this assumption and the use of data about tylosis formation in this connection, and there is abundant supporting evidence from the studies of other workers.

Klein (1923) performed a series of careful experiments on tylosis formation, and after consideration of the possible factors involved, concluded that only the fact of whether the parenchyma cells bordering on the vessels are in contact with air or water is responsible for whether tyloses are formed or not. That is, growth is initiated in a region where a primary wall (pit membrane) is in contact with an abundance of moist air. The vessel provides a sterile chamber in which the air is maintained presumably in a near saturated condition sufficient to prevent the drying of the pit membrane. The protoplast of the living cell has access to a relatively unlimited supply of oxygen and growth proceeds vigorously.

Priestley (1929) studied the sequence of changes in the shoot of the flowering plant, and found that, whether a living cell plays its part as a meristematic unit, or as a vacuolating, dividing cell, or makes its last contribution to growth in the form of a final extension in volume, seems to depend on its immediate environment. If the cell is surrounded by an aqueous medium over a limited pH range, it may be meristematic. Over a wider range it may be vacuolated, but still capable of growth and division, but when the surrounding sap is displaced by air, a period of rapid extension occurs before it enters into a stable state as part of the permanent tissues of the plant. In this case the extension of the cell is limited by the simultaneous growth of the neighbouring cells, and the limited air space surrounding the cells, but it is significant that the rapid increase in growth is concurrent with the replacement of sap in the intercellular spaces with air. The moist primary wall undergoes limited expansion as the enclosed protoplast gains access to a limited increase in available oxygen.

In heartwood formation, a similar situation prevails. The sap-filled vessels become non-conducting and their cavities fill with air. In the presence of so much moisture the air would be nearly saturated. The living protoplasts in contact with the air cavity are stimulated to growth, which may express itself in tylosis formation if the pits are large enough or, if not, in enhanced metabolic activity producing end-products which may be excreted.

Wounds allow access of air around the cells and wound tissue is produced. In fact, it seems that where a living protoplast bounded by a primary wall is in contact with wet air, an enormous increase in growth rate occurs. Cleavage of the early wood fibres, exposing living ray cells to a sterile air-filled cavity therefore provides these cells with a stimulus for active growth, which expresses itself in different ways in the three species according to the anatomical and physiological attributes of the cells.

It is interesting to consider the increased growth stimulus applied to cells by increased availability of oxygen in relation to the conclusions of Thimann (1946). After summarizing the work of numerous investigators on growth hormones, he concluded that growth was controlled, at least in part, by specific processes in respiration. The enhanced growth of unrestricted ray cells after exposure to moist air is consistent with this conclusion, and suggests that, in trees, the limitation of available oxygen for respiration immediately on the xylem side of the cambium is a physiological factor contributing to normal tree form.

IV. CONCLUSIONS

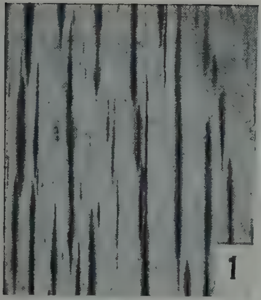
(1) Adverse growth conditions during late wood formation in standing conifers may cause partial collapse of the thin-walled early wood tracheids, and radial cleavage in the early wood.

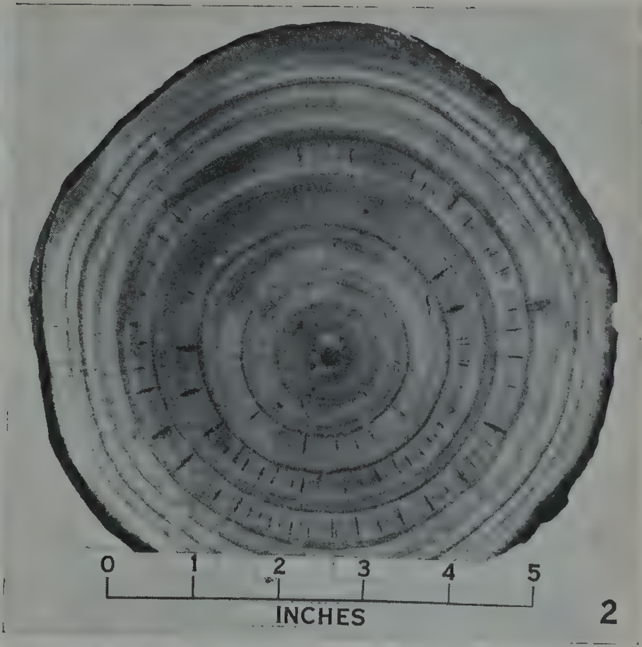
(2) After cleavage, living ray parenchyma cells are exposed to a cavity which contains nearly saturated air, and is sterile, thereby preventing the drying out of membranes and contamination by microorganisms.

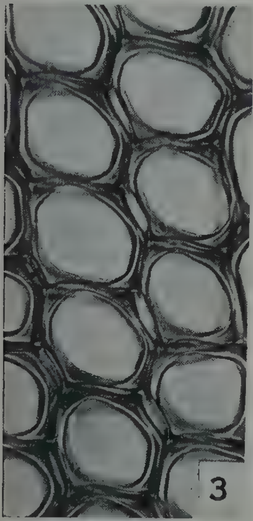
(3) Increased access of air to the living cell acts as a powerful growth stimulus.

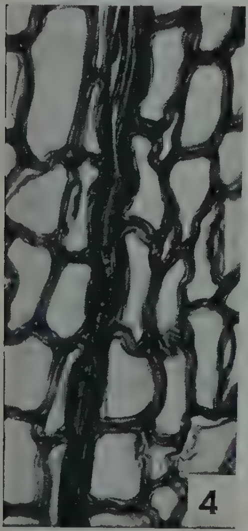
(4) An enhanced metabolic rate occurs, which may express itself in proliferation and growth (radiata pine) or secretion of metabolic end-products (Douglas fir), the type of response being conditioned by the anatomy and physiology of the ray parenchyma cells.

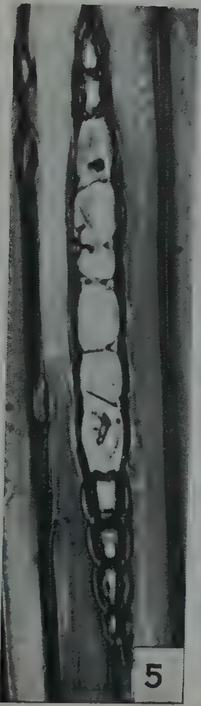
RADIAL FISSURES IN CONIFER WOOD

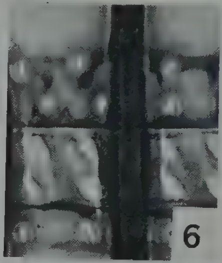

1

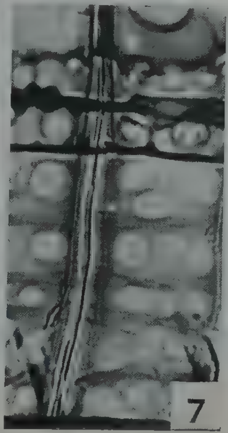

0
1
2
3
4
5
INCHES
2

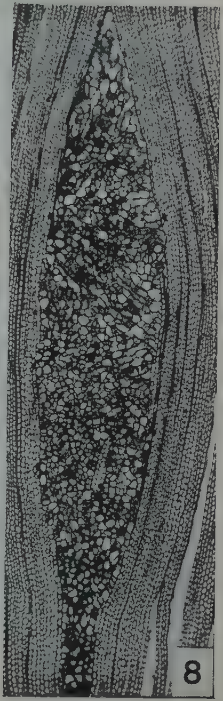

3


4

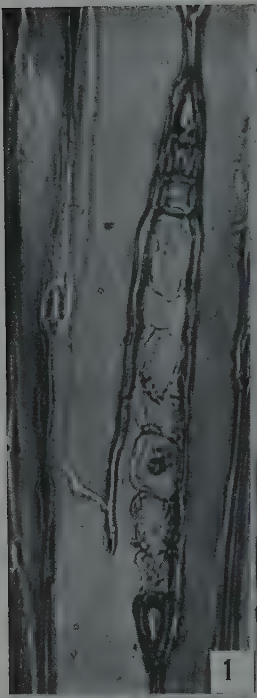

5

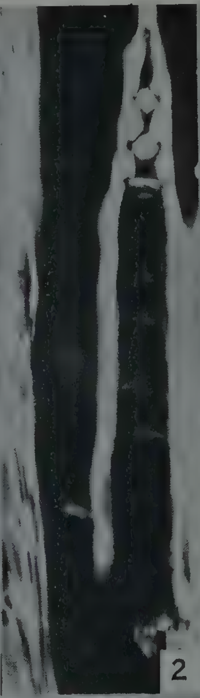

6

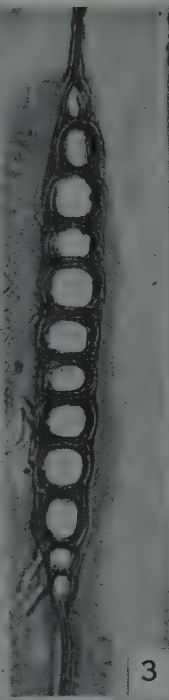

7

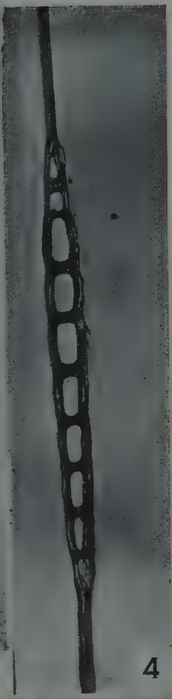

8

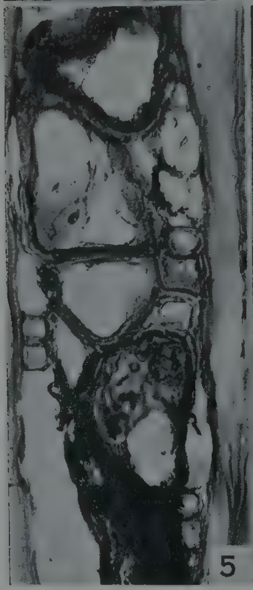
RADIAL FISSURES IN CONIFER WOOD

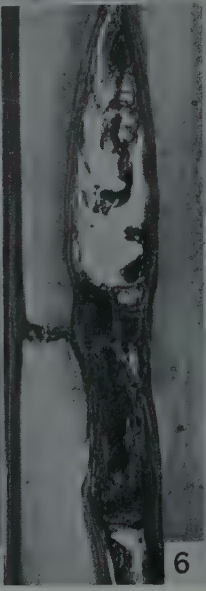

1

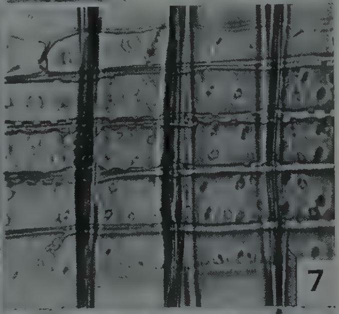

2

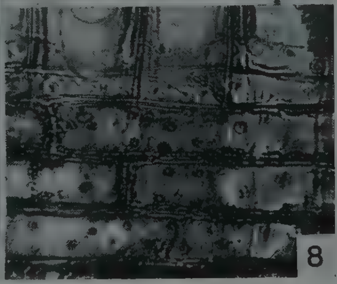

3


4


5


6


7


8

(5) In species where the burst of activity before death of the ray cells produces little contrast between sapwood and heartwood (white spruce), the cavities may remain empty.

V. Acknowledgments

The author gratefully acknowledges the assistance of Mr. B. H. Bednall, Conservator of Forests, and members of the staff of the Woods and Forests Department, South Australia, in supplying material and information concerning it. The encouragement and criticism of Dr. H. E. Dadswell and Dr. M. R. Jacobs are also gratefully acknowledged.

VI. References

Chattaway, M. Margaret (1949).—The development of tyloses and secretion of gum in heartwood formation. *Aust. J. Sci. Res.* B 2 (3): 227.

Day, W. R. (1950).—Report on drought crack of conifers. Imp. For. Inst., Oxford. 12 pp. (mimeo.)

Gerry, E. (1914).—Tyloses, their occurrence and practical significance in some American woods. *J. Agric. Res.* 1 (6): 469.

Jacobs, M. (1946).—The growth stresses of woody stems. For. Timb. Bur. Aust. Bull. No. 28.

Klein, G. (1923).—On the etiology of tyloses. *Z. Bot.* 15: 417.

Kramer, P. J. (1951).—Causes of injury to plants resulting from flooding of the soil. *Plant Physiol.* 26: 722.

Lutz, H. J. (1952).—Occurrence of clefts in the wood of living white spruce in Alaska. *J. For.* 50 (2): 99.

Priestley, J. H. (1929).—Cell growth and cell division in the shoot of the flowering plant. *New Phytologist* 28: 54.

Pryor, L. D. (1947).—Damage to *Pinus radiata* by climatic agents. *Aust. For.* 11: 57.

Reid, J. S., and Mitchell, M. T. (1951).—Internal checks occurring in Douglas fir from two sites. *For. Prod. Res. Notes (N.Z.)* 1 (2): 2.

Thimann, K. V. (1946).—"Currents in Biochemical Research." pp. 321 et seq. (Interscience Publishers Inc.: New York.)

Explanation of Plates 1 and 2

Plate 1

Fig. 1.—*Pinus radiata.* Defect in veneer, surface view. × ½.

Fig. 2.—*Pinus radiata.* Log showing radial checking in the early wood of some growth rings (scale attached).

Fig. 3.—*Pinus radiata.* Normal early wood tracheids. T.S. × 335.

Fig. 4.—*Pinus radiata.* Early wood tracheids between cleavages, showing partial collapse. T.S. × 335.

Fig. 5.—*Pinus radiata.* Ray showing ray tracheids with thickened walls and ray parenchyma with thin primary walls. T.L.S. × 380.

Fig. 6.—*Pinus radiata.* Small ray showing marginal ray tracheids with dentate thickening and bordered pits and ray parenchyma with large simple ray tracheid pitting. R.L.S. × 380.

Fig. 7.—*Pinus radiata.* Ray showing parenchyma with thin walls and large simple ray tracheid pitting. R.L.S. × 380.

Fig. 8.—*Pinus radiata.* Defect, showing cavity filled with abnormal tissue. T.S. × 18.

PLATE 2

Fig. 1.—*Pinus radiata.* Ray with one adjacent fibre wall pulled away to show thin-walled ray parenchyma. T.L.S. × 340.

Fig. 2.—*Pinus radiata.* Same ray photographed between crossed nicols, showing weak birefringence of the ray parenchyma walls, characteristic of primary wall structure. Ray tracheids show strong birefringence characteristic of secondary-thickened walls. T.L.S. × 360.

Fig. 3.—*Pseudotsuga taxifolia.* Ray showing thick-walled parenchyma. × 315.

Fig. 4.—*Picea glauca.* Ray showing thick-walled parenchyma. × 315.

Fig. 5.—*Pinus radiata.* Ray in affected area, showing proliferated ray parenchyma and one group of two ray tracheid series carried to opposite side of fissure. T.L.S. × 300.

Fig. 6.—*Pinus radiata.* Ray at radial limit of cleavage, showing ray parenchyma proliferating into the fissure. T.L.S. × 300.

Fig. 7.—*Picea glauca.* Ray showing thin-walled ray tracheids with bordered pits and thick-walled ray parenchyma with small simple pitting. R.L.S. × 340.

Fig. 8.—*Pseudotsuga taxifolia.* Ray showing thin-walled ray tracheids with bordered pits and thick-walled ray parenchyma with small simple pitting. R.L.S. × 340.

THE EFFECT OF WIND SWAY ON THE FORM AND DEVELOPMENT OF *PINUS RADIATA* D. DON

By M. R. Jacobs*

(*Manuscript received July* 24, 1953)

Summary

The average growth of four series of trees of *Pinus radiata* D. Don, which were prevented from swaying in the wind by the attachment of guy-wires, is compared with the average growth of similar series of free-swaying trees.

Free-swaying trees grew more in diameter over the lower part of the trunk than stayed trees. After 10 yr the increased growth due to sway could be detected to a height on the trunk of between 25 and 30 ft. The effect of sway at a height of 4 ft was greater in a very heavily thinned test area than in a well-stocked test area. Sway caused increased diameter growth of roots near the trunk and increased eccentric trunk development along the line of the main winds. The height growth of the stayed trees was little different from that of the free-swaying trees, but height/diameter relationships were changed. After 2 yr trees that had been prevented from swaying were no longer stable in a normal environment.

When the upper parts of stayed trees were allowed to sway the trees made good use of the factors of the locality for 8 yr. In a series where stayed trees were prevented from swaying throughout their length progressive suppression of diameter and volume increment was observed over 15 yr. Individual reaction to the stimulus of sway appeared to be one of the factors that contributed to the progressive assertion of dominance by certain trees.

I. GENERAL

The Australian Commonwealth Forestry and Timber Bureau commenced an examination of the effect of sway on *Pinus radiata* D. Don in 1936. The study was undertaken because the Inspector General of Forests at the time, Mr. C. E. Lane Poole, considered that the increase in diameter growth which followed very heavy thinning of the species was more than was compatible with the added growing space available to the trees. The author was given the task of examining the anomaly, and in the course of his work investigated the effect of wind sway.

The work on the effect of sway soon gave a likely explanation of some of the increased growth which follows heavy thinning, and the suggestions obtained from the studies up to 1939 were published in Bulletin No. 26 of the Australian Commonwealth Forestry Bureau (Jacobs 1939). Measurements of the experimental plots were continued for periods varying from 6 to 15 yr. The present paper summarizes the indications obtained up to the conclusion of the main tests, and discusses trends that were not apparent in 1939.

---

* Australian Forestry School, Forestry and Timber Bureau, Canberra, A.C.T.

Different investigators have studied the effect of sway on small plants. Ball (1904) found that sway caused a thickening of the walls of cells. Gilchrist (1908) made sunflowers sway and found a marked increase in growth near the base of the plant. Rasdorsky (1925) fixed small plants to a water-wheel to stimulate sway, and found that this increased the diameter growth of the stem. The author has not been able to find records of experimental work on the swaying of plants as large as trees. However, European foresters have maintained for generations that the changing strength requirements of a tree trunk are adjusted through the medium of its reaction to wind.

II. EXPERIMENTAL METHOD

The experimental method used in the main tests was to select a number of comparable pairs of trees, and to prevent one tree of each pair from swaying in the wind over a predetermined portion of the trunk. This was done by fixing suitable guy-wires to cup hooks screwed into the trunk. The second tree of each pair was allowed to sway freely throughout its length. The effect of sway was estimated by comparing the average growth of the series of stayed and free-swaying trees.

In selecting comparable pairs, a number of trees of good form and health equal to twice the number of pairs required was first chosen. The trees were then indexed and their diameter at breast height (4 ft 3 in.) measured. They were then arranged in ascending order of diameter at breast height, and successive pairs bracketed as being comparable. Each member of a pair had grown to a closely similar diameter and was in an approximately similar state of health at the same age. The tree to be stayed in each pair was decided by tossing a coin.

This method of selecting comparable pairs of trees to test the effect of simple treatments has been frequently used in experiments on trees and it has proved satisfactory. It is not certain that trees which have grown at a similar rate in the past will continue to do so, but irregularities in subsequent behaviour are masked if comparisons are restricted to the average responses of the individual members of a number of pairs.

The use of comparable pairs provides data suitable for analysis by the "*t*" test, which has been used to determine the significance of the means presented. Where the "*t*" test indicated that the means are significantly different at the $P = 0.05$ level, the differences are called "significant". Where the "*t*" test indicated significant difference at the $P = 0.01$ level, the differences are called "highly significant".

During the experiments a check was made on the effect on growth of the method of attachment of the guy-wires to the stayed trees. This was done by screwing cup hooks similar to those used to attach the guy-wires into the free-swaying trees. In addition, guy-wires were frequently attached to the base of free-swaying trees. There has been no indication that the cup hooks and guy-wires have had an effect that would influence the conclusions arrived at from the tests.

A fuller description of the appreciable problems encountered in preventing trees from swaying is given in the Bulletin No. 26 referred to above.

III. A Test on the Effect of Sway on the Lower Part of the Trunk in a Heavily Thinned Stand

This test was established in 1937 at Mt. Stromlo plantation, A.C.T., in a compartment well protected from the main storm winds of the district. The compartment had been planted in 1921 at a spacing of 6 by 6 ft. Thirty-seven comparable pairs of trees were selected. The individual trees selected were distributed over a test area of 0.7 ac. After selection of the pairs all other trees on the test area were removed. This represented an extremely heavy thinning, 800 trees being removed and 74 left standing.

After thinning one tree from each pair was stayed with guy-wires at a height of 20 ft, the upper portion of the tree being allowed to sway freely in the wind.

The diameter at breast height at the time of establishment varied from 4.4 to 8.1 in. Diameter growth was measured in all trees by means of steel tapes at the following positions:

1. A band marked on the tree close to ground level;
2. A band marked on the tree at a height of 5 ft;
3. A band marked on the tree at a height of 10 ft;
4. A band marked on the tree at a height of 15 ft;
5. A band marked on the tree a little below the attachment of the guy-wires at 20 ft in the stayed trees and at a similar position in the free-swaying trees;
6. A band marked on the tree a little above the attachment of the guy-wires at 20 ft in the stayed trees, and in a similar position in the free-swaying trees.

The average increment in inches of diameter of the 37 stayed and 37 free-swaying trees at these heights in the first 2 yr following the establishment of the test is given in Table 1.

After the second year it was not possible to maintain the stayed trees in a stable condition with guy-wires at the 20-ft level. Additional guy-wires were added at higher positions where they would keep the trees stable, and the experiment maintained in fair condition until 1945. The upper parts of the stayed trees were always allowed to sway in this test.

Between 1939 and 1945 five pairs of trees were lost to the experiment when stayed trees collapsed after guy-wires broke in storms, but 32 pairs remained at the conclusion of the main part of the test in 1945. Table 2 shows the effect of sway in the lower 15 ft of the trunks between 1937 and 1944.

Discussion of the Test Summarized in Tables 1 *and* 2

The initial diameters given in rows 1 and 2 of Table 2 show that the two series of trees were closely comparable at the commencement of the experiment. Rows 3 and 4 of Table 2 show that during the experiment the free-swaying trees grew considerably more in diameter than the stayed trees up to a height of 15 ft.

The relative increase in increment of the free-swaying trees is greatest near ground level and falls off gradually with height. A tree is an erect cantilever beam. Sway seems to stimulate growth near the junction of the beam with its point of support.

TABLE 1

AVERAGE DIAMETER INCREMENT (IN.) AT DIFFERENT HEIGHTS ON THE TRUNK OF 37 COMPARABLE PAIRS OF STAYED AND FREE-SWAYING TREES OF PINUS RADIATA IN THE FIRST 2 YR AFTER THE STAYED TREES WERE PREVENTED FROM SWAYING OVER THE LOWER 20 FT OF THE TRUNK

Height of Measurement on the Trunk	Near Ground Level	5 Ft	10 Ft	15 Ft	Near Guy-wires at 20 Ft	
					Below Guy-wires	Above Guy-wires
Stayed trees	1.45	1.15	1.22	1.36	1.60	1.81
Free-swaying trees	2.28	1.61	1.52	1.55	1.49	1.46

The differences between the increments are highly significant by the "*t*" test except those immediately below the guy-wires.

When a tree is stayed the point of support of the cantilever beam is lifted to the level of the stays. The above-stay figures in Table 1 show that above the attachment of the guy-wires the stayed trees grew appreciably faster than the free-swaying trees at the same height. This has been found in all tests made by the Bureau. After about 2 yr the increase in diameter of the stayed trees above the attachment of the guy-wires can be seen by eye from the ground.

The slight increase in growth of the stayed trees relative to the free-swaying trees immediately below the guy-wires, as shown in Table 1, is of interest even though the differences are not quite significant over the 2-yr period. This phenomenon has usually been observed in Bureau tests. There is a sympathetic to-and-fro movement of the trunk just below the stays which is opposite in direction to, but synchronized with, the swaying movement above the stays. An observer up the tree on a windy day can feel this movement with his hands. A sinuous movement can be felt all along the stayed portion of a trunk as the upper part sways in the wind.

There seems little doubt that the changing strength requirements of the trunks of *P. radiata* are adjusted through the medium of its reaction to wind. After about 2 yr the trees prevented from swaying were unstable when again exposed to normal wind stresses throughout their length. They tended to blow over or break along the trunk in the first high wind. Evidently the trees must sway as they grow if they are to remain stable.

TABLE 2

AVERAGE DIAMETERS (IN.) AT DIFFERENT HEIGHTS ON THE LOWER PART OF THE TRUNK OF 32 COMPARABLE PAIRS OF STAYED AND FREE-SWAYING TREES IN A VERY HEAVILY THINNED STAND OF PINUS RADIATA AT THE COMMENCEMENT OF THE TESTS IN 1937 AND AFTER 7 YR OF TREATMENT IN 1944, TOGETHER WITH PERTINENT DATA DERIVED FROM THE ORIGINAL FIGURES

Height of Measurement on the Trunk	Near Ground Level	5 Ft	10 Ft	15 Ft
1 Mean diameter stayed trees in 1937	7.11	5.81	5.04	4.59
2 Mean diameter free-swaying trees in 1937	7.21	5.79	5.06	4.67
3 Mean diameter stayed trees in 1944	10.83	9.03	8.23	7.93
4 Mean diameter free-swaying trees in 1944	12.63	10.14	9.07	8.52
5 Average difference in diameter increment 1937-44 between free-swaying and stayed trees	+1.70	+1.13	+0.82	+0.51
6* Average area of the cross section of the stayed trees in 1944 (sq. ft.)	0.653	0.453	0.375	0.348
7* Average area of the cross section of the free-swaying trees in 1944 (sq. ft.)	0.885	0.569	0.456	0.403
8 Average difference in sectional area between free-swaying and stayed trees in 1944	+0.232	+0.116	+0.081	+0.055
9 Increase in increment in sectional area of free-swaying trees (% of sectional area of stayed trees)	36	26	22	16

The differences between the diameter increments of the stayed and free-swaying trees are highly significant at all heights.

* In considering the figures in rows 6 and 7 it should be appreciated that average area of the cross section is not quite the same as the area of the cross section of the average diameter. The areas given in rows 6 and 7 are slightly different from the areas of circles with the diameters given in rows 3 and 4.

IV. TESTS ON THE EFFECT OF SWAY ON THE LOWER PART OF THE TRUNK IN A FULLY STOCKED AND A LIGHTLY THINNED STAND

The experiment summarized in Section III (Tables 1 and 2) showed that sway increases increment in sectional area or diameter over the lower part of the bole, but it does not indicate on its own whether the severity of thinning affects the proportion of additional increment put on by the free-swaying as against the stayed trees. The proportion of additional increment in sectional area put on by the free-swaying trees in the heavily thinned plot is shown in row 9 of Table 2. Information was desired as to the nature of the proportion of increment that could be attributed to sway under conditions of full stocking or lighter thinning.

Experiments similar to the one previously described were established in well-stocked stands adjacent to the first experiment. In these tests five comparable pairs were selected on one side of the first experiment, where the compartment had been thinned to 360 trees per acre, and five pairs were selected on the opposite side where the stocking was around 1000 trees per acre. One tree from each pair was stayed to prevent the lower 30 ft of the trunk from swaying, and one tree from each pair was allowed to sway freely throughout its length. The test was established in 1938 and maintained until 1944. During this period one pair was lost to the experiment from the stand thinned to 360 trees per acre. The growth of the nine remaining pairs is shown in Table 3.

Discussion of the Data of Tables 2 *and* 3

Rows 1 and 2 of Table 3 show that the treated and untreated series were closely comparable at the time of establishment.

Rows 3 and 4 of Table 3 show that the free-swaying trees grew more than the stayed trees over the lower part of the bole. The differences in increment are significant by the "*t*" test up to a height of 12 ft.

Comparison of row 9 in Table 2 with row 9 in Table 3 shows that the proportional increase in increment of the free-swaying trees is much greater in the heavily thinned plot. The difference at breast height is of the order of 26:11. From a forestry viewpoint this was the main information desired from the experiments on sway. It shows that the sharp increase in diameter increment found at breast height after heavy thinning must be regarded with some caution. The increase may not carry on up the tree. Sway has changed the form of the lower part of the bole.

As a matter of interest it is stated that the proportional increment of the four stayed trees in the stand thinned to 360 trees per acre lies between that of the five stayed trees in the stand carrying 1000 trees per acre and that of the stayed trees in the very heavily thinned stand described in Section III, which carried less than 100 trees per acre. Owing to the small number of trees available a quantitative analysis closer than that given in Table 3 is not attempted.

V. A TEST TO FIND THE HEIGHT UP THE BOLE TO WHICH SWAY INFLUENCES DIAMETER GROWTH

This experiment was established in 1938 in Westbourne Woods, A.C.T., in a plantation planted at a spacing of 6 by 6 ft in 1921. Twelve comparable pairs of trees were selected and one tree from each pair stayed at two heights, 14 and 30 ft. In later years the stays were raised higher than 30 ft. This method of staying made the trees stable and it was possible to maintain the experiment until 1948 with the loss of only two pairs. The experimental area had been moderately thinned before the measurements commenced. Growth between 1938 and 1948 is shown in Table 4.

TABLE 3

AVERAGE DIAMETER (IN.) AT DIFFERENT HEIGHTS ON THE LOWER PART OF THE TRUNK OF 9 COMPARABLE PAIRS OF STAYED AND FREE-SWAYING TREES IN A WELL-STOCKED STAND OF PINUS RADIATA AT THE COMMENCEMENT OF TESTS IN 1938 AND AFTER 6 YR OF TREATMENT IN 1944, TOGETHER WITH PERTINENT DATA DERIVED FROM THE ORIGINAL FIGURES

Height of Measurement on the Trunk	Near Ground Level	4 Ft	8 Ft	12 Ft	16 Ft	20 Ft
1 Mean diameter stayed trees in 1938	7.75	6.46	5.75	5.31	4.98	4.62
2 Mean diameter free-swaying trees in 1938	7.95	6.46	5.69	5.20	4.91	4.54
3 Mean diameter stayed trees in 1944	8.59	7.31	6.52	6.05	5.82	5.59
4 Mean diameter free-swaying trees in 1944	9.42	7.71	6.90	6.30	5.99	5.73
5 Average difference in diameter increment 1938-44 between free-swaying and stayed trees	+0.63	+0.40	+0.44	+0.36	+0.24	+0.22
6 Average area of the cross section of the stayed trees in 1944 (sq. ft.)	0.405	0.294	0.233	0.201	0.186	0.172
7 Average area of the cross section of the free-swaying trees in 1944 (sq. ft.)	0.488	0.326	0.262	0.218	0.197	0.181
8 Average difference in sectional area between free-swaying and stayed trees in 1944	+0.083	+0.032	+0.029	+0.017	+0.011	+0.009
9 Increase in increment in sectional area of free-swaying trees (% of sectional area of stayed trees)	20	11	12	8	6	5

TABLE 4

AVERAGE DIAMETERS (IN.) AT DIFFERENT HEIGHTS ON THE LOWER 30 FT OF THE TRUNK OF 10 COMPARABLE PAIRS OF STAYED AND FREE-SWAYING TREES IN A MODERATELY THINNED STAND OF PINUS RADIATA AT THE COMMENCEMENT OF THE TESTS IN 1938 AND AT THE CONCLUSION OF 10 YR OF TREATMENT IN 1948

Height of Measurement on the Trunk	2 Ft	4 Ft	6 Ft	8 Ft	10 Ft	12 Ft	14 Ft	16 Ft
Mean diameter stayed trees 1938	8.12	7.50	6.89	6.52	6.12	5.92	5.69	5.41
Mean diameter free-swaying trees 1938	7.98	7.36	6.94	6.45	6.14	5.90	5.66	5.38
Mean diameter stayed trees 1948	12.09	11.24	10.52	10.01	9.62	9.40	9.22	9.04
Mean diameter free-swaying trees 1948	13.06	12.10	11.49	10.79	10.44	10.18	9.86	9.61
Average difference in diameter increment 1938-48 between free-swaying and stayed trees	+1.11	+1.00	+0.92	+0.85	+0.80	+0.80	+0.67	+0.60

Height of Measurement on the Trunk	18 Ft	20 Ft	22 Ft	24 Ft	26 Ft	28 Ft	30 Ft
Mean diameter stayed trees 1938	5.16	4.80	4.49	4.21	3.93	3.50	3.11
Mean diameter free-swaying trees 1938	5.10	4.79	4.44	4.08	3.72	3.34	2.92
Mean diameter stayed trees 1948	8.81	8.56	8.30	8.10	7.93	7.73	7.63
Mean diameter free-swaying trees 1948	9.38	9.19	8.91	8.55	8.36	8.05	7.70
Average difference in diameter increment 1938-48 between free-swaying and stayed trees	+0.63	+0.64	+0.66	+0.58	+0.64	+0.48	+0.26

Discussion of the Data of Table 4

The figures for 1938 show that the two series were closely comparable at the time of establishment. The differences of increment are significant by the *"t"* test to a height of 12 ft and very nearly but not quite significant from 12 to 28 ft.

Because of the inevitable relationship of growth at a sequence of heights it is reasonable to state that the results of the experiment suggest that sway has had an effect on diameter increment in the course of 10 yr to a height of between 25 and 30 ft up the trunk.

VI. An Attempt to Prevent Trees Swaying Throughout the Length of their Trunk

In the tests described in Sections III, IV, and V the upper parts of the trees were allowed to sway freely in the wind. An experiment was established in 1938 in which an attempt was made to prevent a series of stayed trees from swaying throughout their length. The purposes were to find the effect of complete absence of sway on tree form, and to find if sway had an effect on wood structure and properties.

The selection of pairs in this test was different from that of the other tests. Instead of making a selection of comparable pairs of trees on the basis of equivalent previous growth, a row of 60 4-yr-old pines was selected in the Mt. Stromlo Plantation, A.C.T., and alternate trees were stayed. Adjacent trees were then used as pairs in the analyses. It was comparatively easy to keep the small pines from swaying for the first few years. As the trees grew in height additional stays were added. It proved more difficult to keep them from swaying as they grew bigger. Storms were likely to break odd stays and either cause the collapse of the tree or let it sway until the stays were mended. This happened to several stayed trees. However, the test was maintained in good condition until 1948 and in fair condition for 17 of the original 30 pairs until 1953.

The relative growth of the stayed and free-swaying trees in this test followed a pattern similar to that of the other tests. In addition, another factor has made itself evident, namely a progressively suppressive effect on growth if trees are prevented from swaying throughout their length over a long period. This is shown in column 9 of Table 5.

This test area and its surround had been planted in 1934 at a spacing of 9 by 9 ft, and remained unthinned throughout the 15 yr covered by the experiment.

Discussion of the Data of Table 5

Column 9 of Table 5 shows that, as the duration of the experiment lengthened, the increment in cross-sectional area of the stayed trees became a progressively smaller proportion of the increment of the free-swaying trees. As far as the laying down of conducting tissue was concerned, the trees prevented from swaying became more and more suppressed with time.

TABLE 5

AVERAGE DIAMETERS AND CROSS-SECTIONAL AREAS AT A HEIGHT OF 4 FT OF 17 PAIRS OF STAYED AND FREE-SWAYING TREES FROM AGE 4 TO AGE 19, TOGETHER WITH PERTINENT DATA DERIVED FROM THE FIGURES

		Stayed Trees			Free-swaying Trees			
1. Year	2. Age	3. Mean Diameter	4. Mean Sectional Area	5. Sectional Area Increment	6. Mean Diameter	7. Mean Sectional Area	8. Sectional Area Increment	9. Column 5* / Column 8
1938	4	1.81	0.020		1.89	0.022		
				0.040			0.048	0.83
1940	6	3.24	0.060		3.50	0.070		
				0.053			0.073	0.73
1942	8	4.48	0.113		5.05	0.143		
				0.053			0.074	0.72
1944	10	5.44	0.166		6.24	0.217		
				0.057			0.080	0.71
1946	12	6.32	0.223		7.33	0.297		
				0.049			0.076	0.64
1948	14	6.97	0.272		8.21	0.373		
				0.053			0.082	0.65
1950	16	7.58	0.325		9.06	0.455		
				0.046			0.088	0.52
1953	19	8.10	0.371		9.87	0.543		

* Column 9 gives, in effect, the amount of conducting tissue put on between each date of measurement by the stayed trees (i.e. column 5) represented as a decimal fraction of the amount of conducting tissue put on by the free-swaying trees.

As in Tables 2 and 3, the mean sectional areas are not the same as the sectional areas of the trees with mean diameters.

VII. EFFECT OF SWAY ON HEIGHT AND VOLUME INCREMENT

The figures given in Tables 1 to 5 leave little doubt about the effect of sway on the development of wood along that part of the trunk prevented from swaying. The question arises — what happens to the food materials available to the stayed trees? The series of trees which gave the data summarized in Tables 1-5 had equal opportunities and, presumably, very similar root systems at the start of the tests.

Throughout the experiments a check has been kept on heights, and some measurements have been made on tree volumes. These measurements will now be discussed.

Effect of Sway on Height Increments and Height/Diameter Relationships

The height increments in the heavily thinned plot summarized in Tables 1 and 2 were in favour of the stayed trees after the first 2 yr of the experiment. The 37 stayed trees grew an average of 5.7 ft in height in the 2 yr and the free-swaying trees 5.1 ft. The difference was significant at $P = 0.05$ by the "t" test. After the second year the height increments of the two series were not appreciably or significantly different. In 1945 10 pairs of trees from this test were felled for volume determination purposes. Their heights were accurately measured. The mean height of the 10 stayed trees was 64.3 ft and the 10 free-swaying trees 62.3 ft. The difference would not be significant as between means, but the heights are of interest when the height/diameter relationship is considered.

TABLE 6

AVERAGE HEIGHT/DIAMETER RELATIONSHIPS OF 10 STAYED AND 10 FREE-SWAYING TREES AFTER 8 YR OF TREATMENT IN A VERY HEAVILY THINNED TEST AREA

Age at time of measurement 24 yr

Diameter at Breast Height (in.)	6	7	8	9	10
Stayed trees	54	59	65	70	75
Free-swaying trees	48	53	58.5	63.5	68

The height/diameter relationship of trees in an even-aged stand is frequently determined in forestry work. The true average value is usually represented by a curve in which the height difference between diameter classes decreases with increasing diameter. Over a small range of diameter the relationship could be represented by a straight line without involving much error. Forestry research workers frequently draw a curve by eye through a scatter diagram of a dozen or so points from their experience of the way true mean curves usually go when a large number of measurements are available. The author has done this for the 10 stayed and 10 free-swaying trees under consideration, and the height/diameter relationship in Table 6 is suggested, with full appreciation of its weakness by biometric standards.

It will be seen that the estimated difference between the heights of trees of the same diameter class is between 6 and 7 ft in favour of the stayed trees. This represents a considerable difference in the average form of trees growing in the same environment.

Further data on height/diameter relationships are available from the experiment described in Section VI (Table 5). In this test the heights of 27 pairs of stayed trees and free-swaying trees are available for the period 1938-48. In 1938 the average height of the stayed trees was 8.9 ft and that of the free-swaying trees 9.5 ft. For the first 2 yr the stayed trees grew more in height than the free-swaying trees (8.2 ft against 7.3

ft). The difference is significant by the "t" test at $P = 0.05$. In 1948 the average height of the stayed trees was 45.3 ft and that of the free-swaying trees 46.1 ft. These differences are not significant. A scatter diagram of height against diameter in 1948 indicated that a straight-line regression of height on diameter might be applied to both series rather than an attempt at a curvilinear relationship. These regressions were calculated and gave the equations:

stayed trees: $y = 23.76 + 3.153x$;
free-swaying trees: $y = 21.87 + 3.046x$;

where y = height (ft) in 1948, and x = diameter (in.) in 1948.

The height/diameter table worked out from these equations is shown in Table 7.

TABLE 7

AVERAGE HEIGHT/DIAMETER RELATIONSHIPS OF 27 STAYED AND 27 FREE-SWAYING TREES AFTER 10 YR OF TREATMENT IN AN UNTHINNED TEST AREA

Age at time of measurement 14 yr

Diameter at Breast Height (in.)	5	6	7	8	9	10
Stayed trees	39.5	42.7	45.8	49.0	52.1	55.3
Free-swaying trees	37.1	40.1	43.2	46.2	49.3	52.3

The difference between height for diameter of stayed and free-swaying trees in the experiment discussed in Section VI is not as marked as it was in the test discussed in Section III. It should be noted that the test area of the experiment discussed in Section VI was unthinned, whereas the test area of Section III was very heavily thinned, and the diameter growth attributed to the effect of sway much more pronounced.

Effect of Sway on Volume Growth

Nine of the 10 pairs of trees felled in 1945 from the main test described in Section III (Tables 1 and 2) were examined by the method of stem analysis normally used in growth studies in forestry to find their volume growth from 1937 to 1945. The average volumes and volume increments of these trees are shown in Table 8.

The difference between the volumes and volume increments making up these averages is not appreciable or significant. However, it must be remembered that in this test the upper portions of the crowns of the stayed trees could sway.

In 1953 volumes were measured in the test summarized in Section VI (Table 5). In this test the stayed trees had been prevented from swaying as far as proved practicable throughout their length. In this case the average volume to 4 in. under-bark diameter of the 17 stayed trees used in Table 5 was 7.63 cu. ft. and the average volume of the 17 free-swaying trees was 10.94 cu. ft. The difference in favour of the free-swaying trees is highly significant.

Discussion of Height and Volume Growth

Immediately after healthy trees are prevented from swaying their height increment may be greater than that of comparable free-swaying trees. More evidence would be needed before the author was confident that a firm conclusion could be drawn.

No appreciable or significant difference was found between average height increments of stayed and unstayed trees during the full period of the two main tests, the measurement period extending over 8 yr in one and over 10 yr in the other.

TABLE 8

MEAN VOLUMES AND ANNUAL VOLUME INCREMENTS 1937-44 OF 9 COMPARABLE PAIRS OF STAYED AND FREE-SWAYING TREES OF PINUS RADIATA GROWING IN A VERY HEAVILY THINNED EXPERIMENTAL AREA

The figures refer to the volume of the trunk in cubic feet to an under-bark diameter of 4 in.

	1937		1938		1939		1940		1941		1942		1943		1944
Volume of stayed trees	2.98		4.48		6.29		7.54		9.12		9.93		11.46		12.72
Annual increment		1.50		1.81		1.25		1.58		0.81		1.53		1.26	
Volume of free-swaying trees	2.73		4.25		5.88		7.17		8.90		9.80		11.38		12.69
Annual increment		1.52		1.63		1.29		1.73		0.90		1.58		1.31	

After a number of years an appreciable difference was found between the height/diameter relationships of stayed and free-swaying trees, the stayed trees being higher for the same diameter than the free-swaying trees.

In an experiment where the upper part of the stayed trees could sway, no appreciable or significant difference was found in the volume increment of nine originally comparable pairs of stayed and free-swaying trees during 8 yr of treatment.

In an experiment where the stayed trees were prevented from swaying as far as possible throughout their length, the volume production of the free-swaying trees was considerably and significantly greater than that of the stayed trees after 15 yr of treatment.

The data suggest that if healthy trees are prevented from swaying over part of their height they can still make good use of their environment for several years. If they are totally prevented from swaying their efficiency in competition with free-swaying neighbours is progressively lessened.

VIII. EFFECT OF SWAY ON ROOT DEVELOPMENT

During the early period of the experiment discussed in Section III, measurements of the diameter growth of roots of stayed and free-swaying trees were made. The root measurements indicated that sway increased the diameter growth of roots as far as 2 ft from the base of the trunk. This helps to explain the instability of stayed trees. A brief statement of results to 1939 was given in Bulletin No. 26 (Jacobs 1939).

IX. Effect of Sway on the Development of Eccentricity in the Stem

The cross sections of most tree trunks show some eccentricity of development around the pith. In parts of southern Australia where the prevailing wind is commonly said to be from the westerly quadrant, it is usual to find the long axis of the cross sections of the lower parts of the trunks of pine trees lying along the "prevailing wind direction", with the longer "radius" on the lee side. Most foresters, but not all, have attributed this eccentricity to wind. Those who question the idea point out two facts. Firstly, if wind records are carefully analysed, the so-called "prevailing wind" must be more rigidly defined. In the A.C.T. the winds from the westerly quadrant are usually spoken of as the "prevailing winds". Actually, winds from the easterly quarter prevail in point of view of duration, but more miles of wind come from the west. Secondly, the possible effect of the more severe insolation on the north-west sides of the trunks and the protection enjoyed by the south-east sides must be considered.

In the experiment described in Section III an attempt was made to test the effect of wind on the development of eccentricity. Measurements of stem diameter were made each year by engineers' calipers to marked points on the north-south and east-west axis of each tree at different heights. These measurements were made to the nearest millimetre, and were additional to the tape diameters measured in inches used for the diameter analyses already described.

The figures showing the development of eccentricity from 1937 to 1939, that is, the first 2 yr after a heavy thinning, were discussed in Bulletin No. 26 and the following conclusions were arrived at:

(1) The development of eccentricity is greatest near the base of the trees but could be measured up to a height of at least 10 ft.

(2) In trees which developed eccentricity in a north-south direction there was no difference between stayed and free-swaying trees.

(3) In trees which developed eccentricity along the east-west axis there was a greater development in the free-swaying trees than the stayed trees.

(4) The free-swaying trees developed a proportionately greater amount of eccentricity along the east-west axis than did the stayed trees.

The figures suggested that sway in general, and the greater sway from the west in particular, was a factor in causing eccentricity in the cross sections of the trunks.

These caliper measurements were continued to 1944. The figures for the average caliper diameters and diameter increments between 1937 and 1944 are given in Table 9. While these average figures support the conclusions just made, the difference in dimensions along the two planes is not marked. The trees in this experiment were in a relatively sheltered area and they had particularly good forms.

TABLE 9

AVERAGE DIAMETERS (MM) MEASURED BY CALIPERS ALONG EACH OF THE NORTH-SOUTH AND EAST-WEST AXES ON THE TRUNKS OF 32 COMPARABLE PAIRS OF STAYED AND FREE-SWAYING TREES OF PINUS RADIATA AT THE COMMENCEMENT OF TESTS IN 1937, AND AFTER 7 YR OF TREATMENT IN 1944

Heights of Measurements on Trunk	Near Ground Level	5 Ft	10 Ft	15 Ft
Diameter stayed trees N.-S. axis 1937	174	144	125	115
Diameter free trees N.-S. axis 1937	173	144	125	119
Diameter stayed trees E.-W. axis 1937	177	145	127	116
Diameter free trees E.-W. axis 1937	176	144	127	120
Diameter stayed trees N.-S. axis 1944	261	224	205	197
Diameter free trees N.-S. axis 1944	305	250	224	210
Diameter stayed trees E.-W. axis 1944	269	227	208	200
Diameter free trees E.-W. axis 1944	314	255	229	215
Increment stayed trees N.-S. axis 1937-44	87	80	80	82
Increment free trees N.-S. axis 1937-44	132	106	99	91
Increment stayed trees E.-W. axis 1937-44	92	82	81	84
Increment free trees E.-W. axis 1937-44	138	111	102	95

X. VARIABLE EFFECT OF SWAY ON DIFFERENT INDIVIDUAL TREES

The personal impression gained by the author after 17 yr of close association with the experiments being discussed is that individual trees of *Pinus radiata* react differently to the presence or absence of sway. Some stayed trees seem to be checked severely; others grow very long and thin; others develop in a remarkably vigorous and normal manner apart from the decrease in diameter increment near ground level, and the increase in diameter increment immediately above the stays. It is not possible to support all these impressions with figures from experiments designed for the comparison of differences between means. However, one interesting suggestion presents itself after an examination of the data.

This suggestion is that individual reaction to the stimulus of sway seems to be one of the factors that assists the assertion of dominance by certain trees. An analysis of the figures for the two main tests described in Sections III and VI provides the basis for the suggestion.

On several occasions the author has made use of a scatter diagram relating the diameters or sectional areas of the trees in an experimental plot with the diameters or sectional areas of the same trees after one or several years. Helpful indications of the relative behaviour of trees of different degrees of dominance can be obtained in this way. If such a scatter diagram is made with similar units on each axis, and if there could be no growth at all on any of the trees, all points would fall on a straight line, passing through the zero point of the graph, and having a slope of 45°. If all trees grew the same amount the slope of the line would still be 45°, but the line would be moved along one of the axes and it could be defined by the normal equation for a straight-line graph, namely

$$y = a + bx,$$

where x = the original measurement; y = the subsequent measurement; a = a constant, which in all trees growing the same amount would represent that growth; and b = the regression of y on x, which is, of course, 1 for an angle of 45°.

Now, if instead of all trees growing at the same rate, the bigger trees grow faster than the smaller, the value of b will be greater than 1. If the smaller trees grow the faster b will be less than 1.

A scatter diagram was made showing the relationships of the sectional areas at breast height in 1937 of the 32 stayed trees considered in Table 2 with their sectional areas at breast height in 1944. A similar diagram was made for the free-swaying trees. The dispersion of points showed that a straight-line regression might be applied to the data and these regressions were calculated. Their values were:

stayed trees: $y = 0.099 + 1.88x$;
free-swaying trees: $y = 0.185 + 2.07x$;

where x = sectional area (sq. ft.) at breast height in 1937, and y = sectional area (sq. ft.) at breast height in 1944.

Similar regressions were calculated relating the sectional areas in 1938 and 1948 of the trees considered in Table 5. The values were:

stayed trees: $y = 0.176 + 4.69x$;
free-swaying trees: $y = 0.216 + 7.33x$.

It will be noted that:

(1) The values of b (i.e. the regression factor of y on x) are much higher in the second pair of equations than in the first because the trees were much smaller at the start of the experiment.

(2) In both pairs of equations the value of b is higher for the free-swaying trees than the stayed trees. This means that the bigger trees have taken relatively more advantage of the sway stimulus than the smaller trees in each case.

Discussion of the Effect of Sway on Dominance

Of the two experiments providing the data for this discussion, one covers the period from age 4 to 16, and the other the period from age 16 to 23. Throughout this range of ages the effect of sway has been to increase the disparity between size-classes of the free-swaying trees as against the size-classes of the stayed series. The stayed series developed dominant and subordinate trees, but the free-swaying trees did this to a greater extent. Moreover the larger free-swaying trees became progressively more dominant. It appears that individual ability to take advantage of the stimulus of sway is one of the factors behind this.

While the figures suggest that the varying reaction of individuals to the influence of sway is one of the factors that contributes to dominance in an even-aged stand of *Pinus radiata,* the author wishes to make it quite clear that there is no suggestion that this is the only factor contributing to dominance. Several other factors are known to be involved. These include the effect of seed size in giving the plant an initial advantage which may be maintained, irregular ground preparation, good or bad planting, the presence or absence of competing weeds close to the young plant, chance position within the site where a heavy pile of slash has been burned, the relationship of localized soil conditions to dry or wet years at the time of establishment, and probably aspects of natural vigour other than individual reaction to the effect of sway.

The sway experiments made to date by the Forestry and Timber Bureau have not included a study of the mechanism by which sway might influence diameter growth. If the hands are placed on a tree trunk which is swaying in the wind appreciable movement can be felt in the vital region containing the meristematic tissues. It would be of interest to know how this movement causes additional growth near the junction of the tree beam with its point of support, and why its effect seems to be greater in some individuals than in others.

XI. Acknowledgments

The author wishes to acknowledge the help and advice given by Mr. C. E. Lane Poole, former Inspector General of Forests, during the early years of the experiments, and by Mr. G. J. Rodger, present Director General of the Forestry and Timber Bureau, during recent years. Mr. L. D. Pryor carried out the root studies discussed in Section VIII. Mr. A. Wood has assisted in both the field work and the maintenance of the records throughout the tests.

XII. References

Ball, O. M. (1904).—Der Einfluss von Zug auf die Ausbildung von Festigungsgewebe. *Jb. wiss. Bot.* **39**: 305-54.

Gilchrist, Maude (1908).—Effect of swaying by the wind on the formation of mechanical tissue. *Rep. Mich. Acad. Sci.* **10**: 45.

Jacobs, M. R. (1939).—A study of the effect of sway on trees. Commonw. For. Bur. Aust. Bull. No. 26.

Rasdorsky, W. (1925).—Ueber die Reaction der Pflanze auf mechanische Inanspruchsnahme. *Ber. dtsch. bot. Ges.* **43**: 332-52.

THE CAINOZOIC OCCURRENCE OF ACACIA IN AUSTRALIA

By Isabel C. Cookson*

(*Manuscript received August* 20, 1953)

Summary

The occurrence of pollen grains of *Acacia* in several Victorian late Cainozoic deposits has been recorded.

Two sporomorphs, *Acacia octosporites* and *A. myriosporites*, have been described. Some of the microfossils associated with the *Acacia* sporomorphs have been mentioned.

A table giving the range in size and the number of pollen grains constituting the polyads of 53 species of *Acacia* has been included.

I. Introduction

In view of the large number of species of the genus *Acacia* endemic in Australia, it is surprising that so little is known of its past history in this country. Only three references to possible Australian Tertiary occurrences have been found. One of these is the description of *Acacia meiringii* Johns. from lignitic beds, Henty River, Tasmania, which Johnston (1891) believed to be the phyllode of an *Acacia* closely allied to *Acacia melanoxylon*. Another concerns a single leaf from the leaf beds at Sentinel Rock, Aire coast, Victoria, in which Deane (1904) noted a resemblance to a small type of plurinerve *Acacia* although he did not actually refer it to this genus. The identity of these fossils is open to doubt since in neither case has the morphological resemblance to *Acacia* been supported by anatomical details. The third, the determination by Ewart (1916) of a fragment of fossil wood from Lower Pliocene (Chapman 1921) Deep Leads at Deep Creek, near Daylesford, Vic., as *Acacia melanoxylon* R. Br. seems more reliable.

Recently information of a more positive character has been provided by the discovery of pollen of the *Acacia* type in Victorian Tertiary deposits. The pollen of *Acacia* is unlike that of any other Australian genus and is only paralleled in *Inga*, a native of tropical America and the West Indies (Wodehouse 1935) and a few other extra-Australian members of the Mimosoideae (Erdtman 1952). Since none of these genera has been recorded from Australia it may be assumed that the Victorian fossil pollen represents the genus *Acacia*.

II. Pollen of Recent Species of Acacia

The pollen of *Acacia* has been fully described by Wodehouse (1935). It has the form of small compact, regularly arranged clusters of pollen

---

* Botany Department, University of Melbourne.

grains, the "massulae" of Selling (1947) or "polyads" of Erdtman (1952), each unit of which retains the power of independent germination. According to Selling the number of pollen grains in a polyad ranges from six to 36, but only 8-, 12-, and 16-celled examples have been met with in the Australian species examined (Table 1). These numbers have proved constant for a species.

TABLE 1

GENERAL MORPHOLOGICAL CHARACTERS OF THE POLLEN OF SOME RECENT AUSTRALIAN SPECIES OF ACACIA

Section	Specimen	No. of Grains per Polyad	Longer Equatorial Diameter of Acetolysed Polyads (μ)	Distal Wall of Pollen Grains Crenulate
Aphyllae	*A. alata* R. Br.	16	42-45	+
Continuae	*A. triptera* Benth.	16	37-43	−
Uninerves	*A. acinacea* Lindl.	16	52-57	+
	A. aculeatissima Macbride	12	41-46	+
	A. acanthoclada F. Muell.	16	44-52	−
	A. armata R. Br.	8	39-47	+
	A. aspera Lindl.	12	41-46	+
	A. buxifolia A. Cunn.	16	49-52	+
	A. calamifolia Sweet	16	49-57	+
	A. decipiens R. Br.	12	36-39	−
	A. diffusa Lindl.	16	48-52	+
	A. microcarpa F. Muell.	16	41-44	−
	A. montana Benth.	8	36-46	+
	A. myrtifolia Willd.	8	36-39	+
	A. obliqua A. Cunn.	16	46-49	−
	A. podalyriaefolia A. Cunn.	16	44-49	+
	A. pravissima F. Muell.	16	36-39	+
	A. pugioniformis Wendl.	12	39-44	+
	A. rupicola F. Muell.	8	36-39	+
	A. sclerophylla Lindl.	16	40-48	+
	A. spondylophylla F. Muell.	16	49-57	−
	A. stricta Willd.	16	49-54	+
	A. suaveolens Willd.	16	52-54	+
	A. verniciflua A. Cunn.	16	49-52	+
	A. vestita Ker.	16	44-49	+
	A. victoriae Benth.	16	49-52	−
Plurinerves	*A. colletioides* A. Cunn.	16	49-57	−
	A. havilandii Maiden	16	39-44	−
	A. howittii F. Muell.	16	57-64	+
	A. implexa Benth.	16	35-40	+
	A. lanigera A. Cunn.	12	40-45	−
	A. melanoxylon R. Br.	16	44-52	+
	A. rigens A. Cunn.	16	42-48	+
	A. stenophylla A. Cunn.	16	40-43	+
	A. subporosa F. Muell.	16	52-54	+
	A. trineura F. Muell.	16	48-55	+

TABLE 1 (*Continued*)

Section	Specimen	No. of Grains per Polyad	Longer Equatorial Diameter of Acetolysed Polyads (μ)	Distal Wall of Pollen Grains Crenulate
Juliflorae	*A. cunninghamii* Hook.	16	50-56	−
	A. floribunda Willd.	16	49-54	−
	A. longifolia Willd.	16	57-65	+
	A. longissima Wendl.	16	42-45	−
	A. lysiphloea F. Muell.	16	42-47	−
	A. maidenii F. Muell.	16	40-45	−
	A. mucronata Willd.	16	48-53	+
	A. ocinophylla Benth.	16	42-48	−
	A. oxycedrus Sieb.	16	40-48	−
	A. sophorae R. Br.	16	53-61	−
	A. verticillata Willd.	16	44-52	+
Bipinnatae	*A. baileyana* F. Muell.	16	52-55	+
	A. dealbata Link.	16	52-54	+
	A. decurrens Willd.	16	52-54	+
	A. discolor Willd.	16	49-55	−
	A. mollissima Willd.	16	39-45	+
	A. nigricans R. Br.	12	33-36	+
	A. pentadenia Lindl.	12	33-41	−
	A. polybotrya Benth.	16	39-54	+
	A. pulchella R. Br.	12	31-39	+

Under normal circumstances the polyads remain intact, but during acetolysis they frequently disintegrate into smaller groups or even individual pollen grains. The latter are roughly quadrangular in shape, their distal walls are even or slightly wavy, and several small rather indistinct apertures occur on the lateral and proximal walls.

III. OCCURRENCE OF ACACIA POLLEN IN AUSTRALIAN DEPOSITS

During the palynological examination of Australian Tertiary sediments that has now been in progress for some considerable time, pollen of *Acacia* has only been observed in residues of the younger deposits. So far it has not appeared in preparations of such Early Tertiary beds as the brown coals and associated clays in Victoria and South Australia, and carbonaceous clays at Vegetable Creek, N.S.W., Ouse, Tas., Cootabarlow, S.A., etc. Two alternative explanations for this apparent absence from Palaeogene beds seem possible; either the genus *Acacia* was not represented in the *Nothofagus*-conifer forests known to have covered large areas of Australia during the Early Tertiary period (Cookson 1946; Cookson and Pike 1953*a*, 1953*b*) or it did not become an integral part of the Australian flora as a whole until after the Lower Miocene period. Evidence in hand, though not decisive, favours the second possibility.

The deposits in which *Acacia* pollen has occurred are all situated in Victoria. They are a ligneous clay at Grange Burn near Hamilton, the age of which, according to Gill (1952), is Upper Pliocene; the leaf beds at Sentinel Rock, Aire coast (Singleton 1941), which Dr. O. P. Singleton has verbally stated are underlain by Balcombian clays (Lower Miocene) and overlain by Pleistocene dune limestone; dark and yellow clays from the Stony Creek basin, near Daylesford, of Middle Pliocene age (Coulson 1950), and a dark grey silty Quaternary clay rich in sea shells from the shore-line between Marine Avenue and Dickens Street, St. Kilda, near Melbourne.

IV. Descriptions of Fossil Pollen of the Acacia Type

The number of pollen grains comprising the polyads of living species of *Acacia* seems sufficiently constant for use in the separation of fossil sporomorphs of this type — on this basis two generalized sporomorphs can at present be distinguished in Victorian deposits, one with 8 pollen grains per polyad, the other with 16. The frequencies of both types have been low but particularly so in the Stony Creek occurrence.

Acacia octosporites n. spm.

Plate 1, Figs. 2-4

Polyads composed of 8 grains, circular (*c.* 21-27 μ in diameter) or oblong (*c.* 32 by 37 μ) in polar view. Single grains vary in shape according to their position, central ones quadrangular, about 8 μ in surface view. The exine of the distal wall is relatively thin and even.

Occurrence.—Ligneous clay, Grange Burn, near Hamilton, Vic. (Upper Pliocene, Gill 1952).

Acacia myriosporites n. spm.

Plate 1, Figs. 1, 5-8

Polyads comprised of more than 8 pollen grains (16 in present examples), circular (37-43 μ) or oblong (37-61 by 35-59 μ) in polar view. Grains of central group about 12 μ; distal walls thin and even or slightly indented.

Occurrence.—Ligneous clay, Grange Burn, near Hamilton, Vic. (Upper Pliocene). Sentinel Rock (A.W. 2 of Wilkinson), Aire River, Vic. (above Balcombian clays (Lower Miocene) and beneath Pleistocene dune limestone). Clays at Stony Creek, Daylesford, Vic. (Middle Miocene). Clay at St. Kilda, near Melbourne.

V. Macroscopic and Microscopic Plant Remains Associated with Pollen of the Acacia Type

(*a*) *Clays at Stony Creek, near Daylesford*

(i) *Macroscopic.*—A small collection of plant remains from the dark ligneous clays of the Stony Creek basin was examined by Patton (1928).

The specimens considered included leaves comparable with those of *Eucalyptus viminalis* Labill. and *E. radiata* Sieb. and fern pinnules similar to those of *Polypodium pustulatum* Forst. and *Pteridium aquilinum* Kuhn. In addition the identity of a piece of wood with pits of the type met with in *Phyllocladus* and *Dacrydium* was discussed but no conclusion was reached as to which of these genera it belonged.

(ii) *Microscopic.*—The microfossil content varies somewhat in the different outcrops of the Stony Creek basin. It is relatively high in the dark clays from which *Eucalyptus* leaves have been described and includes the coniferous sporomorphs *Dacrycarpites australiensis* Cookson and Pike (1953*a*), and *Dacrydiumites florinii* Cookson and Pike (1953*b*). The latter occurrence is of interest in connection with the identification of the piece of wood thought, by Patton, to have belonged to either *Phyllocladus* or *Dacrydium.* Pollen grains of *Phyllocladus* have not been observed in this deposit but the sporomorph *Dacrydiumites florinii,* representative of certain species of *Dacrydium,* is relatively numerous.

Amongst the dicotyledonous pollen types is one morphologically similar to the pollen of certain species of *Eucalyptus;* its identity with this genus is supported by the occurrence of macroscopic leaf remains of *Eucalyptus* in the same matrix. Pollen grains of the families Casuarinaceae, Compositae, Haloragaceae, and Proteaceae are also present; the genus *Nothofagus* does not seem to be represented.

Fern spores are relatively numerous and examples of the sporomorph *Gleichenia circinidites* (Cookson 1953*b*) have been observed. Colonies of *Botryococcus braunii* Kütz. (Cookson 1953*a*) and fragments of leaf cuticles are more or less numerous in the various clays.

(*b*) *Ligneous Clay at Grange Burn, near Hamilton*

(*i*) *Macroscopic.*—Leaf remains are infrequent in this deposit and those found have lost all trace of their original structure. One specimen which, in view of the occurrence in the same deposit of the sporomorphs *Acacia octosporites* and *A. myriosporites,* has some significance, is shown in Plate 1, Figures 11 and 12. It contains portions of 3 small, simple, lanceolate leaves, with entire margins and 3 prominent parallel veins, which resemble the phyllodes of certain small-leaved plurinerved *Acacias,* e.g. *A. montana* Bth. (Plate 1, Figs. 13, 14). However, there is no way of determining whether such was their true nature.

(ii) *Microscopic.*—The pollen and spore content of this deposit is high and from it pollen grains of three types of conifers have already been recorded, namely *Araucariacites australis* Cookson and Duigan (1951), *Dacrycarpites australiensis,* and *Dacrydiumites florinii.* Pollen grains of *Casuarina* and the families Myrtaceae (including a eucalyptoid type), Proteaceae, and Haloragaceae are relatively numerous, but those of *Nothofagus* appear to be absent. The sporomorph *Gleichenia circinidites* Cookson and other varieties of fern spore have been observed.

(*c*) *Sentinel Rock Leaf Beds*

(i) *Macroscopic.*—A collection of leaf remains from these beds was described by Deane in 1904. The types included several forms of *Coprosmaepyhllum* Deane, a genus of uncertain affinity, *Persoonia* sp., *Phyllocladus* (a doubtful identification), fern pinnules, and, of special interest in connection with the present record of *Acacia* pollen from this deposit, a small leaf, the venation of which is "that of the parallel-veined plurinerved type of *Acacia*". Deane remarked upon the "singular absence of the various types prevalent in other deposits already dealt with, namely Mornington and Berwick". It is now known that these deposits are older than the Sentinel Rock leaf beds and in contrast to them contain the general microflora characteristic of Australian Early Tertiary sediments.

(ii) *Microscopic.*—The microspore content of the leaf beds is relatively small and is dominated by one type of fern spore (Plate 1, Figs. 17, 18) which closely resembles the spores of *Cyathea australis* (R. Br.) Domin (Plate 1, Figs. 15, 16). The fossil spores are tetrahedral, trilete, about 44-50 μ in equatorial diameter; the branches of the tetrad scar reach the periphery. The exospore is lightly flecked or psilate and about 2.5 μ thick.

The number of dicotyledonous pollen types is small but includes a eucalyptoid form very similar to the one present in the Stony Creek and Hamilton clays. Pollen grains of *Nothofagus* and the several coniferous types that are usually associated with them in Australian Tertiary beds are missing. Since Deane has recorded a leaf of *Phyllocladus* from this bed it is necessary to stress that pollen grains of this or any other coniferous genus have not been observed in the many preparations examined.

Fungal hyphae and fruit bodies of epiphyllous Ascomycetes (Cookson 1947) are common near the base of the leaf beds.

(*d*) *Clay Uncovered during Excavation for a Sea Wall at St. Kilda, near Melbourne*

(i) *Macroscopic.*—No macroscopic plant remains were discovered by the collector of the samples, Mr. H. T. Clifford, of the University of Melbourne.

(ii) *Microscopic.*—The microfossil content is relatively high and includes pollen grains of angiosperms, fern spores, grass cuticles, and a few examples of the planktonic group, the Hystrichosphaerideae (Cookson 1953*a*). Of the pollen grains present a small, many-pored chenopodiaceous type has the highest frequency. Others occurring include pollen grains of *Nothofagus* cf. *cunninghami* Oerst. (Hook.), *Casuarina*, *Banksia*, *Eucalyptus*, *Haloragis*, and the family Gramineae. Spores resembling those of *Cyathea australis* are numerous.

VI. CONCLUSION

It is too early for any conclusion to be drawn regarding the period during which the genus *Acacia* became established in the Australian flora. All the evidence in hand points to a time subsequent to the Lower Miocene — the closest approximation possible at present for the Sentinel Rock leaf beds. This or an even later date is supported by the fact that in all the deposits in which pollen of *Acacia* has occurred it has been accompanied by pollen grains of genera not yet recognized in Early Tertiary sediments.

The microfloras preserved in all three Tertiary deposits considered, although differing from one another in the number of coniferous types they contain, represent forest communities. There is every reason to believe that in the Hamilton and Daylesford regions a mixed conifer-*Eucalyptus* forest was not far removed from the seat of sedimentation. In the Sentinel Rock area, on the other hand, the forest appears to have had a different composition since as yet there is no evidence that *Acacia* and the ferns present were associated with coniferous species.

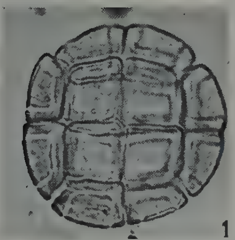
VII. ACKNOWLEDGMENTS

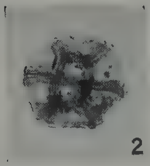
Thanks are gratefully extended to Dr. O. P. Singleton, University of Western Australia, and Mr. H. T. Clifford, University of Melbourne, for geological samples, and to Mr. J. H. Willis and Mr. E. J. Sonenberg for living material of *Acacia*. This work was made possible by financial assistance from the Commonwealth Scientific and Industrial Research Organization and the State Electricity Commission of Victoria.

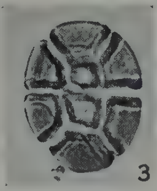
VIII. REFERENCES

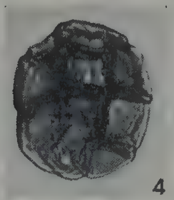
CHAPMAN, F. (1921).—*Vict. Nat.* **37**: 127.
COOKSON, ISABEL C. (1946).—*Proc. Linn. Soc. N.S.W.* **71**: 49.
COOKSON, ISABEL C. (1947).—*Proc. Linn. Soc. N.S.W.* **72**: 207.
COOKSON, ISABEL C. (1953*a*).—Mem. Nat. Mus. Vict. No. 18: 107.
COOKSON, ISABEL C. (1953*b*).—*Aust. J. Bot.* 1 (3): 462.
COOKSON, ISABEL C., and DUIGAN, SUZANNE L. (1951).—*Aust. J. Sci. Res.* B 4 (4): 415.
COOKSON, ISABEL C., and PIKE, KATHLEEN M. (1953*a*).—*Aust. J. Bot.* 1 (1): 71.
COOKSON, ISABEL C., and PIKE, KATHLEEN M. (1953*b*).—*Aust. J. Bot.* 1 (3): 474.
COULSON, A. (1950).—*Proc. Roy. Soc. Vict.* **60**: 157.
DEANE, H. (1904).—*Rec. Geol. Surv. Vict.* 1 (3): 212.
ERDTMAN, G. (1952).—"Pollen Morphology and Plant Taxonomy." (Stockholm.)
EWART, A. J. (1916).—*Vict. Nat.* **33**: 76.
GILL, E. D. (1952).—*Aust. J. Sci.* 15 (2): 47.
JOHNSTON, R. M. (1891).—*Pap. Proc. Roy. Soc. Tasm.* 1891: 11.
PATTON, R. T. (1928).—*Proc. Roy. Soc. Vict.* **40**: 88.
SELLING, O. (1947).—Spec. Publ. Bishop. Mus. No. 38 Gothenberg.
SINGLETON, F. A. (1941).—*Proc. Roy. Soc. Vict.* **53**: 1.
WODEHOUSE, P. G. (1935).—"Pollen Grains." (McGraw-Hill: New York.)

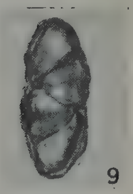
CAINOZOIC ACACIA IN AUSTRALIA

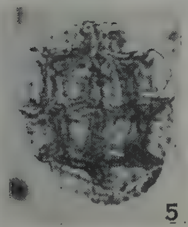

1

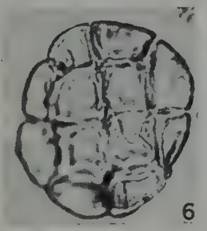

2

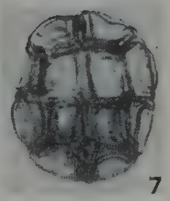

3

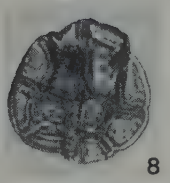

4

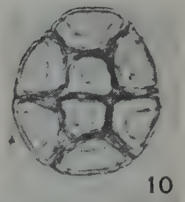

9

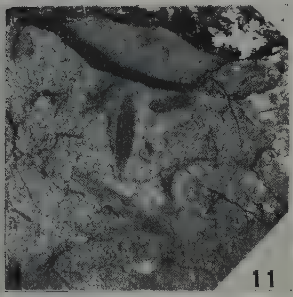

5

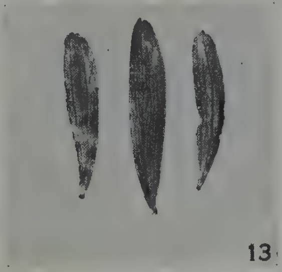

6

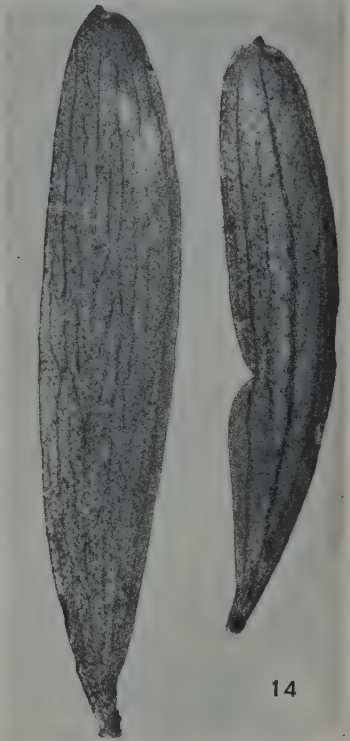

7

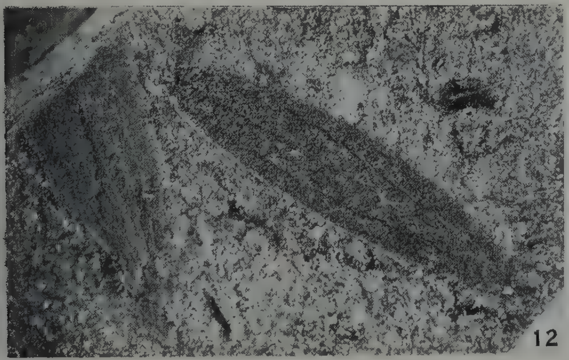

8

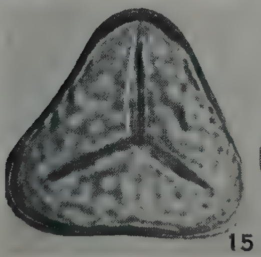

10

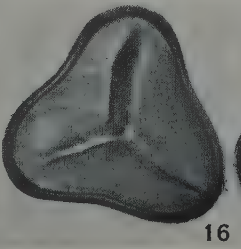

11

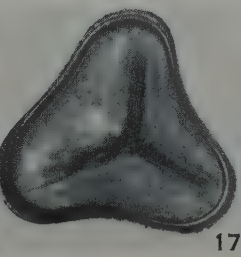

13

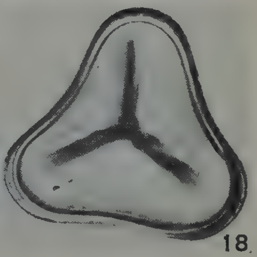

14


12


15


16


17


18

Explanation of Plate 1

Fig. 1.—*Acacia myriosporites.* Hamilton, Vic. × 600.

Figs. 2-4.—*Acacia octosporites.* Hamilton, Vic. × 600.

Figs. 5, 6.—*Acacia myriosporites.* Sentinel Rock, Aire coast, Vic. × 600.

Fig. 7.—*Acacia myriosporites.* Stony Creek, Daylesford, Vic. × 600.

Fig. 8.—*Acacia myriosporites.* St. Kilda, Melbourne, Vic. × 600.

Figs. 9, 10.—*Acacia montana.* Polyads in polar and equatorial views. × 600.

Fig. 11.—Fossil remains resembling phyllodes of a plurinerve *Acacia.* Hamilton, Vic. Natural size. Nat. Mus. Vic. P.15876.

Fig. 12.—Two of the same leaves. × 5.

Fig. 13.—*Acacia montana.* Three phyllodes of a specimen from Whipstick scrub, Bendigo, Vic., in National Herbarium of Victoria. Natural size.

Fig. 14.—*Acacia montana.* Two of the same phyllodes. × 4.

Figs. 15, 16.—*Cyathea australis.* Two acetolysed spores. × 600.

Figs. 17, 18.—Two fossil spores of the *Cyathea australis* type from the Sentinel Rock leaf beds. × 600.

THE FOSSIL OCCURRENCE OF *PHYLLOCLADUS* AND TWO OTHER PODOCARPACEOUS TYPES IN AUSTRALIA

By Isabel C. Cookson* and Kathleen M. Pike*

(*Manuscript received August* 20, 1953)

Summary

Anatomical features which confirm the early Tertiary occurrence of *Phyllocladus* in Australia have been described. *Phyllocladus morwellensis* Deane has been more clearly defined; the sporomorph *Phyllocladus palaeogenicus* has been described and its distribution recorded.

A new sporomorph, *Trisaccites micropterus,* has been established for certain 3-winged fossil pollen grains isolated from Mesozoic and Tertiary deposits.

The distribution of the sporomorph *Microcachryidites antarcticus* Cookson in Australian deposits has been traced.

I. Phyllocladus L. C. and A. Rich

(*a*) *Macroscopic Remains*

The genus *Phyllocladus,* at present restricted in the Australian region to Tasmania and New Guinea, is believed to have existed during the Early Tertiary period in the area that now occupies the south-eastern portion of the continent of Australia. Three fossil species have been described — one from New South Wales and two from Victoria.

The first species to be recognized was *Phyllocladus asplenioides* Ett. (1888) from Oligocene (David 1950, p. 555) Deep Leads near Vegetable Creek (Emmaville), N.S.W. The specimens figured by Ettingshausen, especially the one refigured on Plate 1, Figure 1, through the courtesy of Dr. A. B. Walkom, Director of the Australian Museum, Sydney, resemble so closely the shoots of *Phyllocladus* that their affinity with this genus, although unconfirmed by anatomical details, has not been questioned.

Of the two Victorian species, *Phyllocladus simplex* Deane (1904) from the Sentinel Rock leaf beds, Otway Peninsula, is insufficiently founded to require further consideration. Florin (1940, p. 54) regards the single specimen as "hardly determinable."

The generic relationship of *Phyllocladus morwellensis* Deane, on the other hand, appears to be more certain, the type specimen (Deane 1925, Plate 64, Fig. 17) having the shape and venation of cladodes of *Phyllocladus.* The original material was collected by the late Mr. Henry Deane in company with Mr. W. Baragwanath from the brown coal mine in the Morwell area of eastern Victoria, now known as the Yallourn North Open Cut. However, in recording the occurrence of his new species Deane failed

---

* Botany Department, University of Melbourne.

to publish a specific diagnosis, merely remarking that it has the characteristics of *Phyllocladus* and "differs from the fossil plant from Vegetable Creek, New South Wales."

Recently specimens approximating to the external form of the figured type of *P. morwellensis* and having the structure of the cladodes of *Phyllocladus* have been found in the Yallourn Open Cut (the Yallourn seam overlies the Latrobe seam exposed in the Yallourn North Open Cut). Some structural variations have been found amongst these fossils but until more is known regarding the constancy of similar variations in the living types, it seems advisable that they be referred to one species. They are therefore treated here as additional examples of *Phyllocladus morwellensis* and upon them the description which follows has been based.

(i) *Description of* Phyllocladus morwellensis *Deane*

(1) *External Characters of Cladodes* (Plate 1, Figs. 2-6).—Disconnected cladodes rhomboidal or cuneate, about 10-40 mm long and 4-20 mm wide, sometimes narrowing towards a short stalk-like region; margins entire or lobed, the lobes tending to be distal; veins numerous, obliquely parallel to a rather prominent midrib.

(2) *Cuticular Structure* (Plate 1, Figs. 7, 8, 10).—The cladodes are hypostomatic or have a variable number of stomata on the upper surface.

Lower epidermis (Plate 1, Fig. 8).—The stomata, which are longitudinally oriented, are arranged in more or less regular longitudinal rows. The 2 slightly depressed guard cells are surrounded by a complete ring of 4-6 subsidiary cells, 2 of which are always polar, and approximately the same number of encircling cells which, however, are not clearly distinguishable from ordinary epidermal cells. The subsidiary cells have strongly developed papilla-like outgrowths, which extend along their whole length and form a shallow funnel-shaped outer respiratory cavity.

The epidermal cells are rectangular, with straight inconspicuously pitted lateral walls about 2 μ thick.

Upper epidermis (Plate 1, Fig. 7).—The epidermal cells occur in longitudinal rows. They are square, rectangular, or polygonal and have thickened (2-3 μ), sparingly pitted lateral walls.

(3) *Internal Anatomy* (Plate 1, Figs. 9, 11).—The epidermal cells are square to quadrangular in cross section; their outer walls measure about 4 μ on the upper surface and about 2-3 μ on the lower. There is a single layer of palisade parenchyma beneath the upper epidermis and a zone of spongy parenchyma beneath the lower. In the cortex between the vascular bundles a number of large spaces are present; these appear to be comparable with the "large, lignified, pitted elements" that Robertson (1906) observed in the 3 living species of *Phyllocladus* she examined. Indications of the resin canals, common in living species, have been seen in the fossil cladodes. The detailed structure of the vascular bundles cannot be determined.

(ii) *Comparison of* Phyllocladus morwellensis *with Living and Fossil Species of* Phyllocladus

(1) *Living Species.*—In the structure and arrangement of the stomata, the shape and size of the epidermal cells, the absence of hypodermis, the presence of large lignified pitted elements in the cortex, and in the general external features of the cladodes, *Phyllocladus morwellensis* agrees exactly with the living species of *Phyllocladus.* A special affinity with any particular living species, however, cannot be specified since, as Florin (1931) has already indicated, the species of *Phyllocladus* form a very natural group with uniform cuticular features and a wide variation in the shape and degree of lobing of the cladodes as well as the distribution of the stomata within an individual species.

The differentiation of a distinct palisade layer in the cortex may, if later proved constant, be a more significant character. This feature, which is more or less clearly marked in *P. morwellensis* (Plate 1, Fig. 11) has been observed in the living species *P. glaucus* Carr, *P. hypophyllus* Hook. f., *P. major* Pilg., and *P. trichomanoides* Don. but not in either *P. alpinus* Hook. f. or *P. rhomboidalis* Richard. The agreement, in this respect, between *P. morwellensis* and the two New Guinea species *P. hypophyllus* and *P. major,* and its divergence from the Tasmanian representative *P. rhomboidalis,* are of interest in view of the close geographical approximation of the latter species. However, considerably more material than is at present available will be needed before the taxonomic importance of this feature can be estimated.

(2) *Fossil Species.*—The individual cladodes of *Phyllocladus morwellensis* seem to be distinct from those of *P. asplenioides* in the degree and type of lobing. In *P. asplenioides* the lobes are more numerous, extending from near the base to the apex, and are more acutely pointed.

(*b*) *Fossil Pollen Grains of* Phyllocladus

Fossil pollen grains resembling those of living species of *Phyllocladus* have been recognized in several Australian and Tasmanian Tertiary deposits, but unlike the coniferous sporomorphs *Dacrydiumites florinii* (Cookson and Pike 1953) and *D. mawsonii* (Cookson 1953*b*) they are both inconspicuous and infrequent.

The pollen grains of living species of *Phyllocladus* (Cranwell 1940; Erdtman 1943; Cookson 1947) have small, thin-walled bodies, inconspicuous frill-like wings, and, when fully expanded, wide furrows. Acetolysed examples frequently occur in the unexpanded condition, with the 2 usually pleated wings almost covering the distal surface of the grain. Since it is in this condition that the fossil *Phyllocladus*-like pollen grains are usually found accurate measurements of the body and overall lengths of the fossil grains cannot be specified. However, when the widths of unexpanded pollen grains of the living species of *Phyllocladus* are compared with those of the fossil type, they are found to be of the same order, as also are the size and texture of the wings, the thickness of the exine, and sculpture of the cap. In view, therefore, of this close approximation and the occurrence of the fossil pollen type in both deposits in which macroscopic remains of *Phyllocladus* have been found, there seems no doubt that the grains in question are those of either one or both of the fossil species of *Phyllocladus*.

The pollen grains of the living species of *Phyllocladus* are remarkably uniform and it would be extremely difficult, if not impossible, to separate individual types from a mixture of several. It is presumed that the same uniformity existed amongst the pollen grains of Tertiary representatives, in fact the pollen grains associated with *Phyllocladus asplenioides* in the clay at Vegetable Creek are not appreciably different from those isolated from the Yallourn coal containing *P. morwellensis*. For this reason fossil pollen grains of the *Phyllocladus* type, irrespective of their origin, have been included in one sporomorph, *Phyllocladus palaeogenicus*, described below.

Phyllocladus palaeogenicus n. spm.

Plate 2, Figs. 1-6

(i) *Description.*—Grains ellipsoidal, *c.* 25-35 μ wide (Cranwell 1940, p. 2B) when unexpanded, with 2 narrow frill-like bladders, 4-6 μ deep, which extend almost the entire length of the wide furrow. Exine of cap about *?* μ, finely rugulate.

(ii) *Distribution.*—The asterisk indicates deposits in which megascopic remains of *Phyllocladus* have occurred:

NEW SOUTH WALES: *Vegetable Creek (Emmaville). Mudstone from Deep Leads. Melb. Univ. Geol. Dept. No. 242. Age: Oligocene.

VICTORIA: Yallourn. Ligneous clay from fruit zone near floor of Open Cut. *Brown coal at various horizons in the Open Cut. Age: Oligocene.

Balcombe Bay. Mudstone containing leaf remains, from coastal cliff. Age: Pre-Lower Miocene.

Lal Lal. Ligneous clay from Vic. Mines Dept. bore 62 at 325 ft. Age: Early Tertiary.

Anglesea. Carbonaceous sandstone in coastal cliff, near mouth of Anglesea River. Age: ? Middle Eocene, according to Raggatt and Crespin (1952).

Birregurra. Ligneous clay from Vic. Mines Dept. bore 1 at 760 ft; 823-824 ft. Age: Tertiary.

TASMANIA: Ouse. Lignitic seam in Ouse River about 400 yd upstream from Bridge Hotel. Age: ? Oligocene.

Trevallyn. Pre-basaltic clay from bore 2003 at 36-37 ft and 70-81 ft; investigation bore for the tailrace excavations for the Trevallyn Power Station. Age: ? Oligocene.

SOUTH AUSTRALIA: Cootabarlow, near Lake Frome. Carbonaceous shale. S.A. Dept. of Mines bore at 515-537 ft. Age: ? Early Tertiary.

Pidinga. Lignite from S.A. Dept. of Mines bore P 15 at 35 ft 6 in.-41 ft 6 in. Age: Tertiary.

(iii) *Remarks.*—In the Australian area pollen grains of *Phyllocladus* have, as yet, only been isolated from deposits of approximately Oligocene age. However, in view of the present occurrence of *Phyllocladus* in Tasmania, it seems likely that subsequent work will considerably extend this time range.

Couper (1951) states that "*Phyllocladus* appears to have had a long history in New Zealand, for pollens identical with those of the living species are present in the Upper Cretaceous."

II. TRISACCITES n. spt.

The sporotype *Trisaccites* is proposed for constantly 3-winged fossil pollen grains which cannot be identified with the pollen of any living species.

TRISACCITES MICROPTERUS n. spm.

Plate 2, Figs. 21-29

(i) *Description.*—Body of grains triangular to circular in polar view, according to the degree of expansion, about 20-45 μ in diameter. Bladders 3, rudimentary, frill-like when unexpanded, 4-6 μ deep, broadly inserted around a wide furrow. Exine thin, 1-2 μ over the cap, rather finely granular; internal thickenings of bladders forming an indistinct, fine-meshed reticulum.

(ii) *Remarks.*—The triangular outline of this sporomorph (due to its frequent occurrence in the unexpanded or partially expanded condition) and the constant development of 3 narrow, broadly attached bladders with inconspicuous reticulations, distinguish these grains from those of all other living or fossil coniferous types. In the form and attachment of the bladders and the wide furrow they closely resemble pollen grains of *Phyllocladus*, the number of bladders being the only distinguishing feature. Normally pollen grains of *Phyllocladus* are 2-winged but Cranwell (1941) has mentioned the occurrence of 3-winged forms in pollen samples of *P. glaucus*. During this investigation 3-winged examples have been observed in pollen preparations of *P. rhomboidalis*. It seems possible, therefore, that some connection may have existed between *Phyllocladus* and the extinct podocarpaceous species from which the sporomorph *Trisaccites micropterus* was derived.

The New Zealand pollen type *Dacrydium microsaccatum* described by Couper (1953) from Upper Cretaceous coal measures appears to be remarkably like *Trisaccites micropterus* and it seems probable they are closely related, if not identical. However, as the descriptions stand, the two forms are distinguished by the arrangement of the fibrous thickenings present in the air bladders. In *Dacrydium microsaccatum* they are said to be strongly developed and radial whereas in *Trisaccites micropterus* they form a fine-meshed reticulum. This character has often been difficult to see when the bladders are unexpanded and "frill"-like as they are in the specimen illustrated by Couper in his Plate 4, Figure 38. There is no structural evidence for a connection of the Australian form with *Dacrydium.*

That the species represented by this sporomorph must have had a wide geographical distribution and time range in the Australian region during the Mesozoic and Early Tertiary period is indicated by the occurrence of *T. micropterus* in Jurassic black coal at Wonthaggi, Vic.; Lower Cretaceous deposits in New South Wales and Queensland; and Early Tertiary deposits in the Denmark area of Western Australia and in Tasmania. It appears to have become extinct during the Palaeogene.

(iii) *Distribution.*—The asterisk denotes deposits in which this sporomorph is abundant:

QUEENSLAND: Styx River, near Rockhampton. Black coal. Queensland Geol. Surv. Bore N.S. 13 at 501-505 ft; in coal at top of working seam. Age: Lower Cretaceous (Walkom 1919).

Burrum Coalfield, near Maryborough. Black coal. Jubilee Colliery, in working seam. Age: Lower Cretaceous (Walkom 1919).

NEW SOUTH WALES: Onepah Station, Tibooburra, north-western N.S.W. Marine shale. Age: Lower Cretaceous (*fide* H. Fletcher, Aust. Mus. Sydney).

* Vegetable Creek (Emmaville). Mudstone from Deep Leads. Melb. Univ. Geol. Dept. No. 242. Age: Oligocene.

VICTORIA: Anglesea. Carbonaceous sandstone in coastal cliff near mouth of Anglesea River. Age: ? Middle Eocene (Raggatt and Crespin 1952).

Castle Cove, Aire coast. Basal carbonaceous sandy shale. Age: Upper Eocene or older (*fide* O. P. Singleton).

Lal Lal. Ligneous clay from Vic. Mines Dept. Bore 62 at 325 ft. Age: Early Tertiary.

Bambra. Lignite, Vic. Mines Dept. Bore at 106-110 ft. Age: Early Tertiary.

Birregurra. Vic. Mines Dept. bore 1 at 842-843, 1006-1009, and 1019-1021 ft. Age: Early Tertiary.

Wensleydale. Clay parting in coal. Age: Early Tertiary. G.S.V. 50083.

Eastern View. Carbonaceous shale, Coal Mine Ck., 100 yd upstream from Great Ocean Road. Age: Lower Eocene (Raggatt and Crespin 1952).

Balcombe Bay. Mudstone containing leaf remains, from coastal cliff. Age: Pre-Lower Miocene.

Wonthaggi. Black coal. Age: Jurassic.

TASMANIA: Ouse. Lignitic seam in Ouse River about 400 yd upstream from Bridge Hotel. Age: ? Oligocene.

* Trevallyn. Pre-basaltic clay from bore 2003 at 36-37 ft and 70-81 ft; investigation bore for the tailrace excavations for the Trevallyn Power Station. Age: ? Oligocene.

SOUTH AUSTRALIA: Cootabarlow. Carbonaceous shale. S.A. Dept. of Mines bore at 515-537 ft. Age: ? Early Tertiary.

Pidinga. Lignite from S.A. Dept. of Mines bore P15 at 35 ft 6 in.-41 ft 6 in. Age: Tertiary.

Comaum. S.A. Dept. of Mines bore at 619 ft 6 in. Age: Early Tertiary (Cookson 1953*a*); 674 ft. Age: ? Jurassic (Cookson 1953*a*).

Canopus Station, near the S.A.-N.S.W. border, *c.* 45 miles north of the River Murray. Carbonaceous sands from S.A. Dept. of Mines bore 1 at 900-910 ft. Age: Pre-Upper Oligocene (*fide* S. B. Dickenson).

WESTERN AUSTRALIA: Hay-Denmark railway, deviation at 354 miles. Carbonaceous sandy deposit, 50 ft below surface, "coffee rock". Geol. Dept. Univ. W.A. No. 8662/9. Age: Tertiary.

Nornalup Inlet. Lignite. Geol. Dept. Univ. W. A. No. 32982. Age: Tertiary.

III. MICROCACHRYIDITES ANTARCTICUS Cookson

Plate 2, Figs. 8-20

This sporomorph was first introduced (Cookson 1947) for medium-sized fossil pollen grains with 2 or more short, deep wings, from ligneous deposits at the Kerguelen Archipelago, which are morphologically similar to the grains of *Microcachrys tetragona* Hook. f. (Plate 2, Fig. 7). At that time mention was made of its occurrence in Australian sediments but individual localities were not specified. Since then pollen grains of the *Microcachryidites antarcticus* type have been observed in a relatively large number of Australian deposits. Unlike the Kerguelen examples in which 2-winged forms were numerous, the majority have had 3 wings, although 2- and 4-winged forms have also been seen.

The chronological range of *M. antarcticus* is similar to that of *Trisaccites micropterus.* It has been observed in Jurassic black coal at Wonthaggi, Vic., in beds that are believed to be Jurassic in the Comaum bore, S.A., and through the Lower and Upper Cretaceous to the Oligocene. Couper (1952) has identified *M. antarcticus* from the Lower Cretaceous to Lower Oligocene of New Zealand. A closely similar type has been described by Rao (1943) from the Jurassic of the Rajmahal Hills, India, under the name *Podosporites tripakshi.*

NEW SOUTH WALES: Onepah Station, north-western N.S.W. Marine shale. Age: Lower Cretaceous (*fide* H. Fletcher, Aust. Mus., Sydney).

Vegetable Creek (Emmaville). Mudstone from Deep Leads. Melb. Univ. Geol. Dept. No. 242. Age: Oligocene.

Kiandra. New Chum Hill. Soft ligneous shale 135 ft below the basalt. Dr. Dulhunty's coal sample No. 103. Nat. Mus. Vic. No. P. 15710. Age: Early Tertiary.

VICTORIA: Anglesea. Carbonaceous sandstone in coastal cliff near mouth of Anglesea River. Age: ? Middle Eocene (Raggatt and Crespin 1952).

Lal Lal. Vic. Mines Dept. bore 62 at 187 ft; bore 51 at 398 ft. Age: Early Tertiary.

Birregurra. Vic. Mines Dept. bore 1 at 842-843, 1006-1009, 1019-1021, and 1102-1103 ft. Age: Early Tertiary.

Gellibrand River near Pt. Ronald. Carbonaceous sandy shale 13 ft above beach level. Age: ? Oligocene (Baker 1953).

Wonthaggi. Black coal. Age: Jurassic.

TASMANIA: Ouse. Lignitic seam in Ouse River about 400 yd upstream from Bridge Hotel. Age: ? Oligocene.

Trevallyn. Pre-basaltic clay from bore 2003 at 36-37 ft and 70-81 ft; investigation bore for the tailrace excavations for the Trevallyn Power Station. Age: Oligocene.

SOUTH AUSTRALIA: Cootabarlow. Carbonaceous shale. S.A. Dept. of Mines bore at 515-537 ft. Age: Early Tertiary.

Pidinga. Lignite from S.A. Dept. of Mines bore P15 at 35 ft 6 in.-41 ft 6 in. Age: Tertiary.

Comaum bore at 651 ft. Age: ? Jurassic.

Moorlands brown coal. Age: ? Oligocene.

WESTERN AUSTRALIA: Hay-Denmark railway, deviation at 354 miles. Carbonaceous sandy deposit, 50 ft below surface, "coffee rock". Geol. Dept. Univ. W.A. No. 8662/9. Age: Tertiary.

IV. ACKNOWLEDGMENTS

Thanks are due to Dr. W. Curtis, University of Tasmania, and Mr. T. E. Burns of Launceston, Tasmania, for living material. Mr. H. Fletcher, Australian Museum, Sydney, and Mr. C. C. Morton, Geological Survey of Queensland, kindly provided geological samples from new localities.

Considerable financial assistance has been received from the Commonwealth Scientific and Industrial Research Organization and the State Electricity Commission of Victoria.

V. REFERENCES

BAKER, G. (1953).—Mem. Nat. Mus. Vict. No. 18: 125.

COOKSON, ISABEL C. (1947).—Brit. Aust. N.Z. Ant. Res. Exped. Rep. A 2 (8): 129-42.

COOKSON, ISABEL C. (1953*a*).—*Aust. J. Bot.* 1 (3): 462.

COOKSON, ISABEL C. (1953*b*).—*Aust. J. Bot.* 1 (1): 64-70.

COOKSON, ISABEL C., and PIKE, KATHLEEN M. (1953).—*Aust. J. Bot.* 1 (1): 71-82.

COUPER, R. A. (1951).—*N.Z. Sci. Rev.* 9 (1-2): 10-12.

COUPER, R. A. (1952).—*N.Z. J. Sci. Tech.* B 34: 106-17.

COUPER, R. A. (1953).—Geol. Surv. N.Z. Paleont. Bull. No. 22: 1-77.

CRANWELL, LUCY M. (1940).—*N.Z. J. Sci. Tech.* 22: 1B-17B.

DAVID, T. W. E. (1950).—"The Geology of the Commonwealth of Australia." (Edward Arnold and Co.: London.)

DEANE, H. (1904).—*Rec. Geol. Surv. Vict.* 1 (3): 212-15.

DEANE, H. (1925).—*Rec. Geol. Surv. Vict.* 4: 489-92.

ERDTMAN, G. (1943).—"An Introduction to Pollen Analysis." (Chronica Botanica Co.: U.S.A.)

ETTINGSHAUSEN, C. VON (1888).—Mem. Geol. Surv. N.S.W. No. 2 (189 pp.).

FLORIN, R. (1931).—*K. Svenska VetenskAkad. Handl.* 10 (1).

FLORIN, R. (1940).—*K. Svenska VetenskAkad. Handl.* 19 (2): 5.

RAGGATT, H. G., and CRESPIN, IRENE (1952).—*Aust. J. Sci.* 14: 143.

RAO, A. R. (1943).—*Proc. Indian Acad. Sci.* 13 (3): 181-97.

ROBERTSON, AGNES (1906).—*Ann. Bot.* 20: 259-65.

WALKOM, A. B. (1919).—Qd. Geol. Surv. Publ. No. 263: 7-76.

EXPLANATION OF PLATES 1 AND 2

All the photographs are from untouched negatives

PLATE 1

Fig. 1.—*Phyllocladus asplenioides* Ett. A shoot. Natural size. Australian Museum, Sydney.

Fig. 2.—*P. morwellensis*. Deane's type specimen. Yallourn, Vic. Natural size. Nat. Mus. Vic. No. P. 15869.

Figs. 3, 4.—*P. morwellensis*. Additional examples from Yallourn, Vic. × 2 and natural size. Nat. Mus. Vic. Nos. P. 15870, 15871 respectively.

Fig. 5.—*P. morwellensis.* Portion of a shoot. Natural size. Nat. Mus. Vic. No. P. 15872.

Fig. 6.—*P. morwellensis.* Specimen showing the lobing of the distal region. Natural size. Nat. Mus. Vic. No. P. 15873.

Figs. 7, 8.—*P. morwellensis.* Cuticle from the upper and lower surfaces of a cladode, respectively. × 150. Nat. Mus. Vic. No. P. 15874.

Fig. 9.—*P. morwellensis.* A stoma in transverse section. × 600. Nat. Mus. Vic. No. P. 15875.

Fig. 10.—*P. morwellensis.* A stomatal group in a surface view. × 600. Nat. Mus. Vic. No. P. 15874.

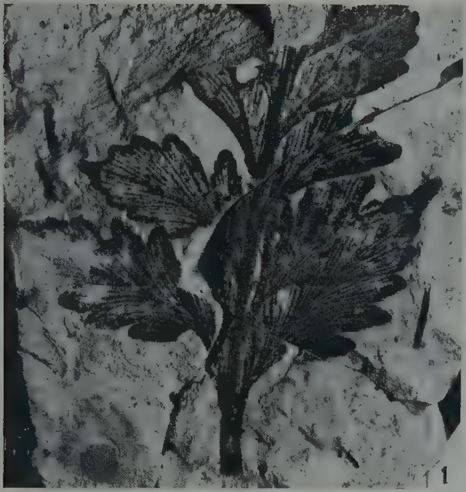
Fig. 11.—*P. morwellensis.* Transverse section of a cladode, showing palisade parenchyma, large ligneous elements, and stomata on the lower surface. × 150. Nat. Mus. Vic. No. P. 15875.

PLATE 2

The pollen grains are magnified 600 diameters

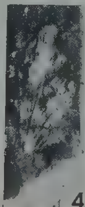
Fig. 1.—*Phyllocladus palaeogenicus.* Pidinga, S.A.
Fig. 2.—*P. palaeogenicus.* Vegetable Ck., N.S.W.
Fig. 3.—*P. palaeogenicus.* Birregurra, Vic.
Fig. 4.—*P. palaeogenicus.* Yallourn, Vic.
Figs. 5, 6.—*P. palaeogenicus.* Two views of the same grain; Yallourn, Vic.
Fig. 7.—*Microcachrys tetragona.* A grain in polar view. Cradle Mountain, Tas.
Fig. 8.—*Microcachryidites antarcticus.* Styx Coalfield, Queensland.
Figs. 9, 10.—*M. antarcticus.* Onepah Station, N.S.W.
Figs. 11, 12.—*M. antarcticus.* Comaum, S.A.
Figs. 13, 14.—*M. antarcticus.* Vegetable Ck., N.S.W.
Fig. 15.—*M. antarcticus.* Pidinga, S.A.
Fig. 16.—*M. antarcticus.* Cootabarlow, S.A.
Fig. 17.—*M. antarcticus.* Lal Lal, Vic.
Fig. 18.—*M. antarcticus.* Trevallyn, Tas.
Fig. 19.—*M. antarcticus.* Hay-Denmark, W.A.
Fig. 20.—*M. antarcticus.* Stony Ck., Daylesford, Vic.
Fig. 21.—*Trisaccites micropterus.* Wonthaggi, Vic.
Fig. 22.—*T. micropterus.* Onepah Station, N.S.W.
Fig. 23.—*T. micropterus.* Eastern View, Vic.
Fig. 24.—*T. micropterus.* Pidinga, S.A.
Figs. 25, 26.—*T. micropterus.* Ouse, Tas.
Fig. 27.—*T. micropterus.* Vegetable Ck., N.S.W.
Fig. 28.—*T. micropterus.* Hay-Denmark, W.A.
Fig. 29.—*T. micropterus.* Birregurra, Vic.

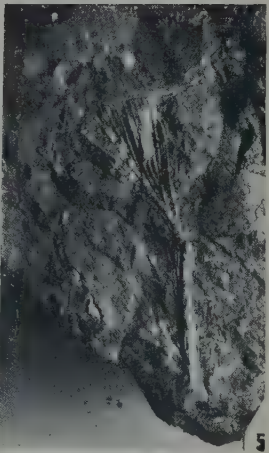
FOSSIL PHYLLOCLADUS IN AUSTRALIA

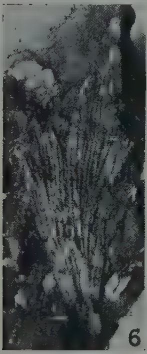

1

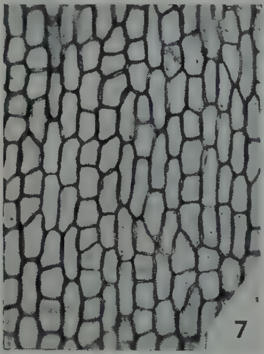
2

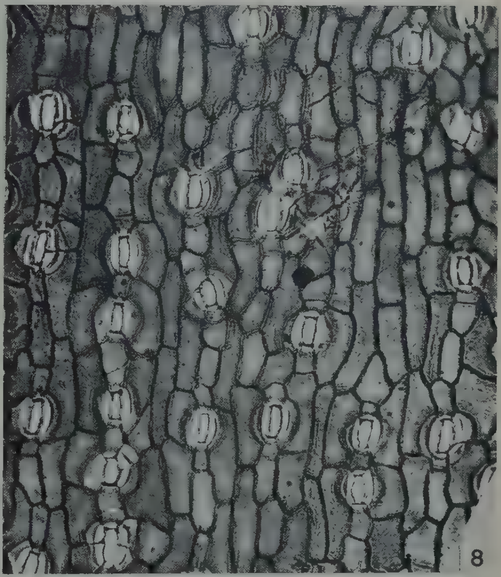
3

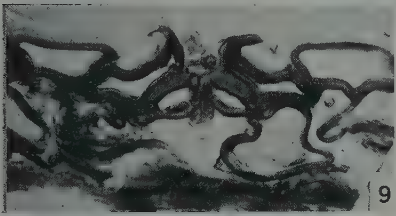

4

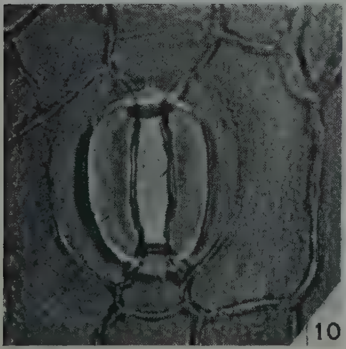

5

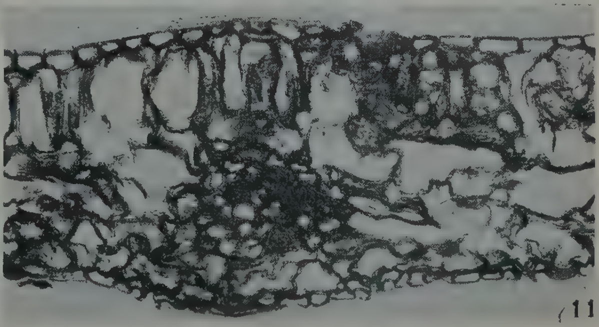

6


7

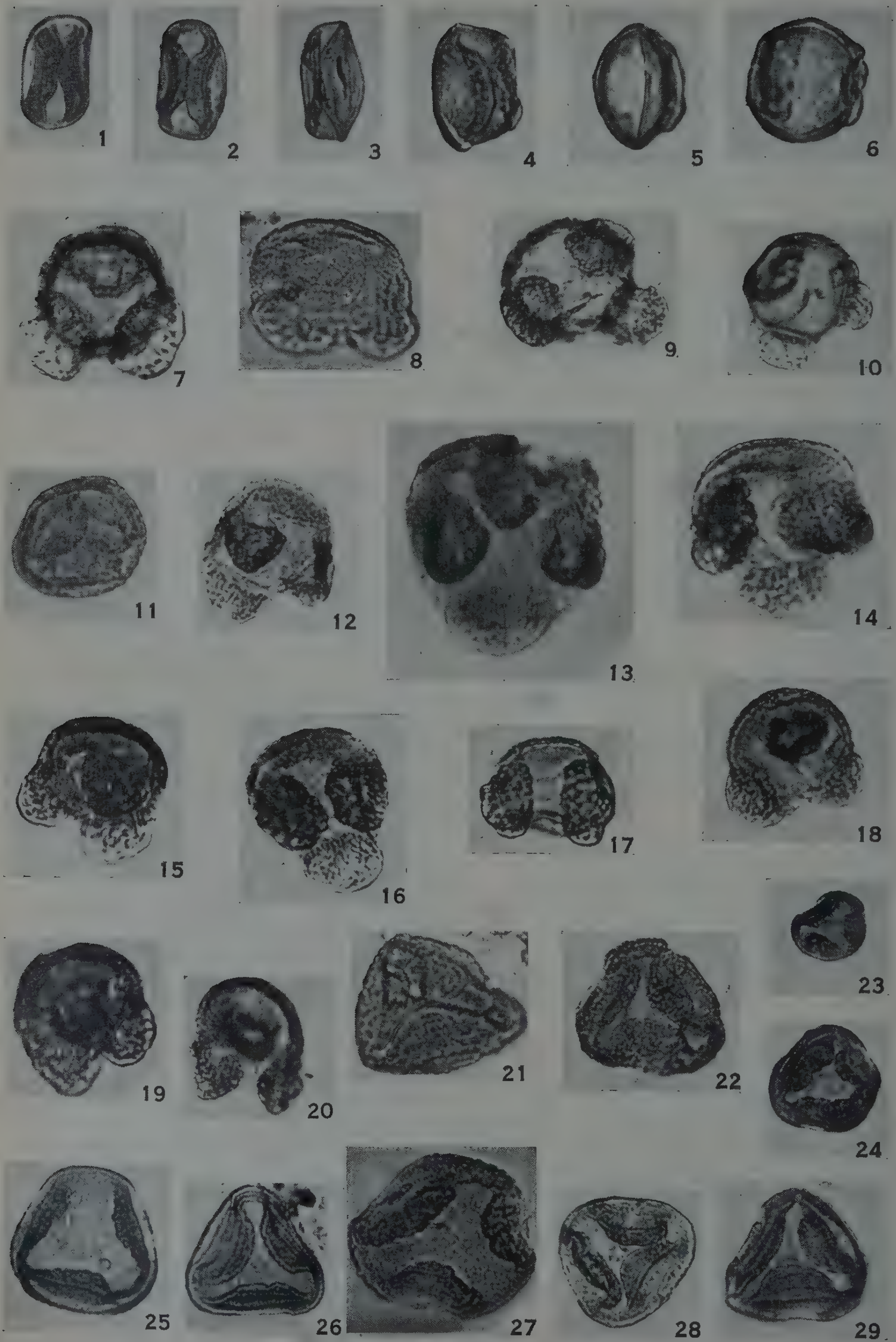

8


9


10


11

FOSSIL PHYLLOCLADUS IN AUSTRALIA


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29

AUTECOLOGY OF SOME NATURAL PASTURE SPECIES AT TRANGIE, N.S.W.

By E. F. Biddiscombe*, E. G. Cuthbertson†, and R. J. Hutchings*

(*Manuscript received August* 13, 1953)

Summary

Features of the autecology of four native perennial grasses (*Stipa*, *Chloris*, and *Digitaria* spp.) and an important group of winter annual species are reported from a 5-yr study of a natural pasture at Trangie, N.S.W. The investigation was mainly concerned with the response of the species to changes in seasonal climatic conditions.

The study period (1948-52) was relatively moist (mean annual rainfall 25.6 in.) and the growing season (May-November) longer than average. Available moisture showed considerable variation in autumn and spring, and was the primary factor in the variable success of germination and seedling survival among the perennial grasses.

Plant development in the perennial grasses is discussed for three study intervals, March 1948-50 (above average rainfall), March 1950-51 (recurrent flooding over 8 months), and March 1951-52 (including a long, dry summer); in all periods striking fluctuations were noted in persistency and basal area of established plants, particularly the small plants of each species.

Available moisture is advanced as the principal factor controlling seasonal distribution of green forage production by the perennial grasses, temperature becoming limiting only at midwinter (June-July). All species conformed to a similar production pattern, showing a midsummer minimum (except in January 1951), late summer and spring peaks, and a midwinter trough.

Flowering and maturation periods are listed for the perennial grasses, and infrequent but heavy seed production recorded for all species. Characteristic features of the root systems are discussed in relation to drought resistance and response to effective rainfall.

Germination of *Medicago* spp. was most frequent in May and June (1-in. soil temperature 51-61°F), but was also successful in March, April, and July. *Erodium cygnorum* and *Hordeum leporinum* favoured late February to early May (65-75°F) for germination. Among high populations percentage seedling survival was low, even in a very favourable season.

Given adequate winter moisture (as in 1948 and 1949), *Medicago* spp. and *E. cygnorum* showed virtually an exponential increase in green forage production between May and September. The level of September production of these species is shown to be correlated with moisture availability in April.

The principal factors ensuring regular recurrence of the winter annuals in pastures of the Trangie environment are outlined and discussed.

I. Introduction and Review of Literature

The autecological features of some important natural pasture species have been studied at the Trangie Agricultural Experiment Station in central western New South Wales. The studies occupied 5 yr (1948-52

---

* Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T.
† Division of Plant Industry, Department of Agriculture, Sydney.

inclusive), and formed part of a sheep grazing experiment conducted jointly by C.S.I.R.O. and the Department of Agriculture, New South Wales.

Four native perennial grasses are treated: *Stipa falcata* Hughes, *Chloris acicularis* Lindl., *Chloris truncata* R. Br., *Digitaria coenicola* (F. Muell.) Hughes. Five winter annual species are studied: *Medicago hispida* Gaertn. var. *denticulata* Urb., *M. minima* L., *M. laciniata* Mill., *Erodium cygnorum* Nees, and *Hordeum leporinum* Link. The *Medicago* species are usually treated as a composite group. Taxonomic descriptions of all species are given by Black (1943).

Early literature concerning the perennial grasses includes the work of Maiden (1889) and Turner (1895) who noted the general distribution, drought resistance, and recognized pastoral value of *Chloris acicularis, C. truncata,* and *Stipa* spp. Breakwell (1923) elaborated on the same aspects. Detailed autecological studies of native grasses of arid southern Australia are confined to the work by Osborn, Wood, and Paltridge (1931) on *Stipa nitida* S. & H. In the Trangie district, distribution of the grasses in relation to soil and vegetation has been studied by Key (1945) and Clark (1948). The surveys by Beadle (1948) in the western districts and Moore (1953) in the south-eastern Riverina showed that the grasses are widely distributed over the interior of New South Wales. *Chloris acicularis* and *Digitaria coenicola* are of greater importance in central and northern inland areas, while *C. truncata* and *Stipa falcata* extend also to southern regions as common species.

Erodium cygnorum is native to Australia, and *Medicago* spp. and *Hordeum leporinum* are exotics which rapidly achieved a wide distribution in western New South Wales following settlement. *H. leporinum* was introduced into New South Wales probably about 1880 (Breakwell 1921). Clark (1948) considered that *Medicago* spp. were introduced into the Trangie district with the advent of sheep grazing in the period 1870-1880, and that *H. leporinum* first appeared there following the drought of 1902. He noted the importance of the winter annual species in grazed pastures at "Bundemar", 20 miles north-east of Trangie. According to Beadle (1948), *E. cygnorum* is a valuable fodder plant extending to many parts of the far west and north-west of the State, while *Medicago* spp. attain more importance east of the Darling River; *H. leporinum* is more common in the wheat belt and adjacent pastoral country.

The community of the present study was situated on light-textured soil and was dominated throughout the experimental period by *Stipa falcata* and *Chloris acicularis,* with a variable development of the winter annual component. In these respects the pasture was a typical disclimax produced by many years of relatively light grazing (Biddiscombe 1953).

II. METHODS

Botanical composition of the perennial grass communities on three soil types was derived from density and basal area recordings (Table 2, Fig. 1) on random quadrats (2 by 1 m). By means of an area-list method (Hanson and Love 1930), living plants were counted individually, and their diameter measured 1 cm above ground. Basal area was expressed as a percentage of quadrat area. The total area and the number of quadrats sampled on each soil were: sand — 47 ac, 60 quadrats; sandy loam — 77, 110; loam — 98, 130.

Botanical composition in relation to tree and shrub cover (Table 3, Fig. 1) was evaluated in a similar manner. On 5 ac of sandy soil, density and basal area measurements from 30 quadrats among *Callitris glauca* R. Br. (height 30-35 ft, average density 1 tree per sq. ch.) were compared with recordings from 30 quadrats in an adjoining treeless area. On 4 ac of loam soil, the comparison lay between the pasture in stands of *Apophyllum anomalum* F. Muell. (height 8-10 ft, average density 4 shrubs per sq. ch.) and that of nearby cleared areas; 25 quadrats were examined in each situation. Pasture on obvious sheep camping sites was not sampled.

Pantograph quadrats (1 by 1 m) at 18 permanent sites on sand and loam soils were charted annually for the period March 1948-50 as a method of evaluating seedling survival and plant development of the perennial grasses (Figs. 4 and 5). As a result of flooding in 1950 only 12 sites remained for a similar study of development during March 1951-52. Development of established plants was followed for three arbitrary size groups, comprising small plants (basal diameter 1-3 cm), medium plants (3.5-6.5 cm), and large plants (> 6.5 cm).

Immediate flood effect on the perennial grasses was determined in May 1950 (Table 7). Areas of shallow flooding (2-5 in. submergence for 2-3 days) and deep flooding (5-9 in. for 5-6 days) were sampled. Counts of single living and dead plants were taken from 25 quadrats (2 by 2 lk) at fixed intervals along transects commenced and directed at random. Symptoms of flood damage were clearly distinguishable in the brown discoloration of leaves, stems, and basal shoots, and the rotted nature of the roots.

The period March 1950-51 gave an account of plant development in response to recurrent flooding followed by low summer rainfall; basal area changes were measured on 32 permanent quadrats (2 by 1 m) in deep-flood and non-flood situations (Fig. 6).

The study sites described above for seedling survival and plant development were open to grazing (1 sheep to 2 ac) throughout the period.

Seasonal distribution of green forage production was determined from the quantity of green material present at 2-monthly intervals (Fig. 7). The data were a valid index of seasonal variation in vigour of growth, but did not give absolute production over defined periods because of the presence of the grazing animal. Perennial grasses were studied over 4 yr (March 1948-52), the sampling series being complete except for May 1950 when floods prevented transport of requisite equipment to the area.

Stipa falcata and *Chloris acicularis* were sampled on the one area (24 ac of sandy loam), and *Digitaria coenicola* and *Chloris truncata* on separate areas (12 ac). These study sites were selected on the following criteria: test species relatively prominent each year; similar mean basal area of associated perennial grasses during the period; sites not flooded in 1950; same stocking rate (1 sheep to 2 ac). Production of *Erodium cygnorum* and *Medicago* spp. (Fig. 12) was compared as an average of two winter periods (1948 and 1949) on the same study site as *Stipa falcata*. *Hordeum leporinum* was not studied because its sporadic occurrence precluded an adequate sampling.

At each sampling 8-16 quadrats (5 by 5 lk) were cut on the 12-ac sites and 16-32 on the 24-ac sites, the greater intensity being applied when green forage was scarce. Quadrats were located by pacing along predetermined random coordinates based on fence-lines. Percentage botanical composition of the green forage was estimated on each quadrat, and the material cut at ground level. All weights were taken on oven-dry material.

Nitrogen content was determined by Kjeldahl digestion; composite samples were taken of the above-ground parts of numerous ungrazed plants at the same growth stage. Crude protein content (Tables 8 and 12) was calculated from the standard formula, percentage nitrogen × 6.25.

Phenological data (Figs. 8 and 14) were compiled by regular, detailed note-taking on the whole community, including small areas exclosed from grazing.

Root penetration (Figs. 9 and 15) was examined *in situ* by the hydraulic method of Stoeckeler and Kluender (1938). All species except *Hordeum leporinum* were growing on a sandy soil with light clay commencing at a depth of 17-24 in. Roots of *H. leporinum* were studied on a clay loam. The adult plants of each species were equal in basal diameter (perennials) or similar in foliage development (annuals), and each plant was distant 3-4 ft from any other along the trench face.

Root density of each perennial species (Fig. 9) was determined as the average for two adult plants of equal diameter. Six-in. cores of soil and roots were extracted to a depth of 36 in. below crown centre, using a standard soil auger (dia. 3.5 in.). A 12-in. core below 36 in. completed the sampling. Root density of annual species (Fig. 15) was examined beneath the centre of pure stands containing 6-8 adult plants. Soil monoliths (8 by 8 in.) were removed from each 6-in. zone to a depth of 30 in. In order to minimize the factor of unequal exposure to competition, all single plants (perennials) or stands of plants (annuals) were selected at a distance of 4-5 ft from other plants. All samples were cleaned by a soil-elution method similar to that of Upchurch (1951). The oven-dry weight of roots in each zone was expressed as a percentage of total root weight.

Viability of *Medicago* seed (chiefly set in 1947) was determined on four soil types for the period 1948-51 (Fig. 10). Two closed quadrats (5 by 5 lk) were originally matched in amount of burr, and permanently located on each soil. *Medicago* seedlings were counted and removed following each germinating rain. Other plants were not disturbed, and tin barriers were erected to prevent reseeding of the quadrats. Seasonal distribution of germination for the years 1948 to 1950 (Fig. 11) was calculated from the above counts; the distribution in subsequent years was determined from a second set of quadrats examined in a similar manner.

Seedling survival of *Erodium cygnorum* and *Medicago* spp. on sand and loam soils (Table 10) was investigated in 1952 by means of plant counts at two exclosure sites on each soil. Seedlings on 12 1-lk squares of each quadrat (5 by 5 lk) were counted and removed after each germination period; those on alternate squares of the quadrat were allowed to reach maturity before being counted.

III. The Habitat and the Pasture Community

The studies were conducted on 220 ac of almost flat country having a uniform fall of 1 in 75 to the north-west. Downes (1947) has described the texture and pH profiles of the three principal soil types (Table 1), and has classified the soils as red-brown earths derived from alluvial parent material. A small area of a fourth type — a brownish grey clay loam of cloddy structure (pH 6.3) — has been studied only in relation to germination of *Medicago* spp.

Table 1

TEXTURE AND pH PROFILES OF THREE SOIL TYPES

Soil Type	Depth (in.)	Texture	Reaction (pH)
Greyish brown to brown sand	0-5	Sand	6.1
	5-19	Sand to sandy clay loam	6.4-8.1
	19-45	Light clay	8.4
Greyish brown sandy loam	0-8	Sandy loam	6.7
	8-18	Sandy clay loam	7.6-8.4
	18-48	Light clay	8.6
Greyish brown loam	0-8	Loam	7.4
	8-12	Sandy clay loam	8.4
	12-54	Light clay	8.5

Thin, irregular stands of *Callitris glauca* on sandy or sandy loam soil and *Apophyllum anomalum* on loam soil constituted the principal tree vegetation remaining on the area. *Eucalyptus populifolia* Hook. and *Heterodendron oleifolium* Desf. were sparse.

The pasture community formed an open stand of tussocky perennial grasses contributing 2-3 per cent. basal area. The *Stipa*, *Chloris*, and *Digitaria* spp. under study comprised a high proportion of the population.

Subsidiary perennials occurring throughout the pasture included *Stipa setacea* R. Br., *Eragrostis lacunaria* F. Muell., *Aristida jerichoensis* Domin, and *A. behriana* F. Muell. A vigorous development of winter annuals occurred during most winters, *Erodium cygnorum* being invariably the dominant in this phase of the pasture. *Medicago minima* and *M. laciniata* were also common on all soils, while *M. hispida* var. *denticulata* became prominent only on clay loam soil. Wet summers gave a second active phase of annual species, principally *Eragrostis cilianensis* (All.) Link and *Solanum esuriale* Lindl.

TABLE 2

DENSITY AND TOTAL BASAL AREA OF PERENNIAL GRASSES ON THREE SOIL TYPES, MARCH 1948

Mean of 60, 110, and 130 random quadrats respectively on sand, sandy loam, and loam soils

Species	Density (plants/sq. m.)		
	Sand	Sandy Loam	Loam
Stipa falcata	9.4	9.0	8.2
Chloris acicularis	4.4	7.4	4.6
Digitaria coenicola	25.1	3.3	0.8
Miscellaneous species	7.1	4.5	8.1
Total density	46.0	24.2	21.7
Total basal area (%)	1.72	1.22	1.15

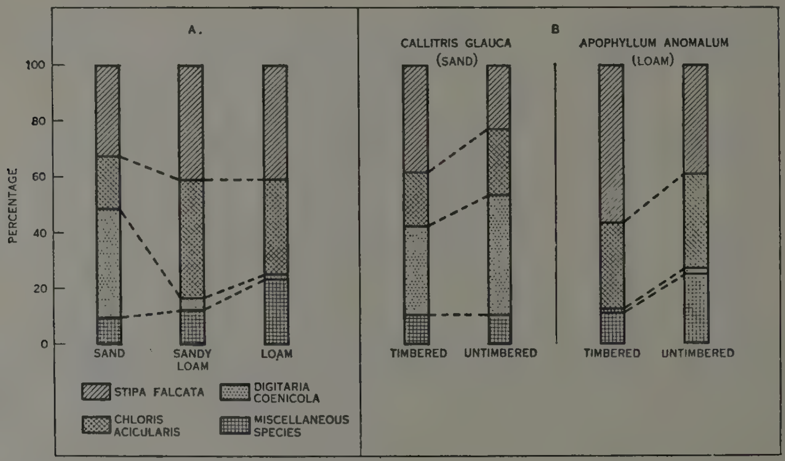


Fig. 1.—Botanical composition (derived from percentage basal area) of perennial grass component in relation to (1*a*) soil type (mean of 60-130 random quadrats) and (1*b*) vegetation cover (25-30 quadrats).

The experimental area previously formed an unfenced section of a larger paddock stocked at approximately 0.8 sheep per acre per annum during the years 1944 to 1947 inclusive. This common pre-treatment of the whole area enabled an assessment of species distribution in relation to soil type to be made at March 1948. As shown by plant density (Table 2) and by percentage contribution to total basal area (Fig. 1*a*), sandy soil showed *Digitaria coenicola* dominance, sandy loam *Stipa falcata-Chloris acicularis* codominance, and loam *S. falcata* dominance.

Vegetation cover, unaltered by clearing for at least 10 yr, was also found to influence the distribution of certain perennial grasses. Presence of *Callitris glauca* on sandy soil was associated with a decrease in *D. coenicola* and an increase in *S. falcata* (Table 3, Fig. 1*b*); the latter was also more prominent among *Apophyllum anomalum* on loam soil.

TABLE 3

DENSITY AND TOTAL BASAL AREA OF PERENNIAL GRASSES OF TIMBERED AND CLEARED SITES ON TWO SOIL TYPES, MARCH 1948

Species	Density (plants/sq. m.)			
	Sand		Loam	
	Timbered*	Untimbered†	Timbered*	Untimbered†
Stipa falcata	10.5	7.5	9.4	7.2
Chloris acicularis	3.8	5.0	3.7	4.7
Digitaria coenicola	22.0	28.6	0.4	1.0
Miscellaneous species	4.5	8.7	5.5	9.1
Total density	40.8	49.8	19.0	22.0
Total basal area (%)	1.57	1.87	1.03	1.18

* Mean of 30 random quadrats.

† Mean of 25 random quadrats.

IV. CLIMATE

Climatic data from various parts of the Trangie district have been discussed previously by Key (1945), Clark (1947*a*, 1947*b*, 1948), and Cuthbertson (1952). This discussion is based on the records maintained at Trangie Agricultural Experiment Station.

Trangie lies within the southern section of the region of summer maximum rainfall although the difference between the seasons is not marked (Fig. 2). The 17-in. mean annual rainfall exhibits a slight summer maximum in the period October to March inclusive. Loewe (1948) using Maurer's average variability index places Trangie in the region of "unfavourably high variability". Cuthbertson (1952), expressing the standard deviation as a percentage of the mean, reports a 42 per cent. variability for the summer period and a 14 per cent. variability for the winter period.

TABLE 4

DEVELOPMENT OF EVAPOTRANSPIRATION (E_t) INDICES FROM MEANS OF PREVAILING CLIMATE AT TRANGIE AGRICULTURAL EXPERIMENT STATION (26 YEARS OF RECORDS)

Index (in.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Potential E_t	4.84	4.69	3.91	2.44	1.60	0.99	0.93	1.06	1.73	2.59	3.49	4.34	32.61
Precipitation	1.48	1.67	1.66	1.45	1.25	1.86	1.32	1.18	1.08	1.31	1.78	1.46	17.50
Storage change	0	0	0	0	0	+0.87	+0.39	+0.12	—0.65	—0.73	0	0	
Storage	0	0	0	0	0	0.87	1.26	1.38	0.73	0	0	0	
Actual E_t	1.48	1.67	1.66	1.45	1.25	0.99	0.93	1.06	1.73	2.04	1.78	1.46	17.50
Water deficiency	3.36	3.02	2.25	0.99	0.35	0	0	0	0	0.55	1.71	2.88	15.11

Water need = 32.61 in. Aridity index 15.11/32.61 = 46.3 per cent. Humidity index = 0. Moisture index = —27.8 per cent. Summer concentration of thermal efficiency = 73.2 per cent. Climatic type D B_2'd c_2'.

TABLE 5

DEVELOPMENT OF EVAPOTRANSPIRATION (E_t) INDICES FROM CLIMATIC MEANS FOR THE 5-YEAR PERIOD ENDED SEPTEMBER 30, 1952 — TRANGIE AGRICULTURAL EXPERIMENT STATION

Index (in.)	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Potential E_t	4.69	4.61	3.76	2.39	1.55	1.08	0.92	1.09	1.69	2.52	3.21	4.30	31.81
Precipitation	1.69	2.77	2.95	1.62	1.67	2.66	1.74	2.05	1.82	2.58	3.24	0.80	25.59
Storage change	—0.20	0	0	0	+0.12	+1.58	+0.82	+0.96	+0.13	+0.06	+0.03	—3.50	
Storage	0	0	0	0	0.12	1.70	2.52	3.48	3.61	3.67	3.70	0.20	
Actual E_t	1.89	2.77	2.95	1.62	1.55	1.08	0.92	1.09	1.69	2.52	3.21	4.30	25.59
Water deficiency	2.80	1.84	0.81	0.77	0	0	0	0	0	0	0	0	6.22

Water need = 31.81 in. Aridity index = 6.22/31.81 = 19.6 per cent. Humidity index = 0. Moisture index = —11.8 per cent. Summer concentration of thermal efficiency = 72.6 per cent. Climatic type C_1 B_2'd c_2'.

Rainfall per wet day is not high, the mean being 30 points (100 points = 1 in.). However, on the average, 59 per cent. of the rainfall is received in daily falls in excess of 50 points, the highest individual falls occurring more frequently in the summer and autumn months.

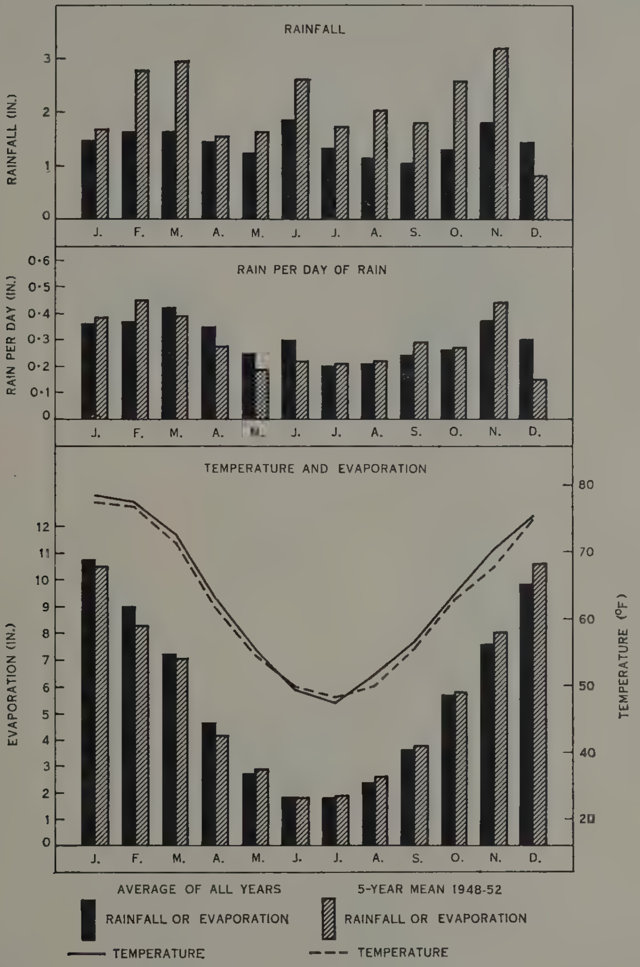


Fig. 2.—Monthly climatic means at Trangie Agricultural Experiment Station, comparing the experimental period (1948-52) with all years of record.

Average temperatures are high, and reach a maximum in January. Frosts are common during the winter months, and minima below freezing point are recorded frequently in June, July, and August. Severe frosts of this nature may occur in September and early October.

Evaporation is high throughout the year, reaching a maximum in January. Only in June does rainfall exceed evaporation.

The climatic regime experienced during the experimental period (Fig. 2) was atypical in that rainfall was phenomenal and culminated in widespread floods during 1950. Comparison between the average regime and that experienced is best made with climatic indices. It is considered that allowance should be made in the Trangie environment for soil water surplus and storage, so that Thornthwaite's (1948) concepts are preferred to precipitation-evaporation ratios. Evapotranspiration (Tables 4 and 5) is calculated from Thornthwaite's formula as modified by Leeper (1950):

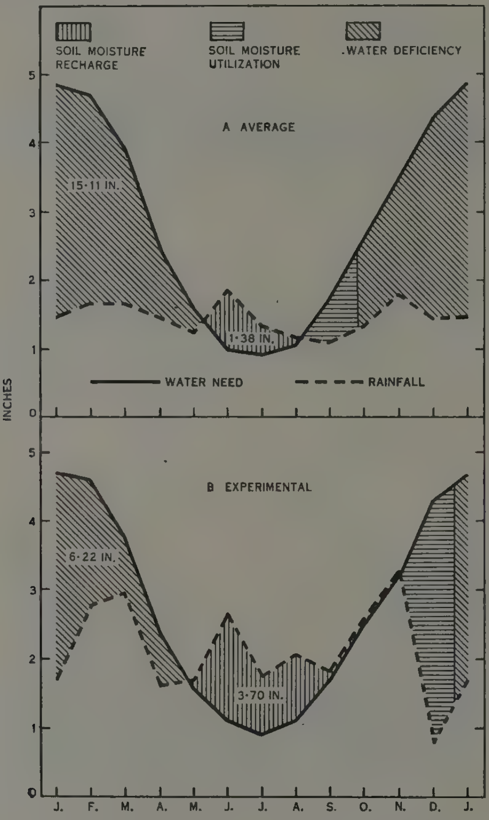


Fig. 3.—Comparison of (*A*) average and (*B*) experimental regimes of potential evapotranspiration (water need).

$$\text{Monthly potential } E_t = 4.4S + (T\text{-}m),$$

where evapotranspiration (E_t) is measured in millimetres, S is the saturated vapour pressure at mean temperature T (°F) of the particular month, and m is the annual mean temperature (°F).

A comparison of potential evapotranspiration (water need) and rainfall received (Fig. 3*A*) shows that Trangie has an average growing season of 4 months when "stored" water is taken into account. The concept presupposes maximum growth potential for the period, so that the actual growing season might reasonably be extended to 6 months on the basis that precipitation in the additional period was sufficient to meet, say, 75 per cent. of the postulated water need. A similar comparison for the experimental period (Fig. 3*B*) reveals a growing season of 8 months, which could be extended to 9 months on the above basis. As a result, early summer and (in some years) autumn production of the pasture exceeded the normal level.

V. AUTECOLOGY OF PERENNIAL GRASSES

(*a*) *Germination, Development, and Persistency*

Seasonal occurrence of vigorous germination during 1948-52 was as follows: *Stipa falcata* — two autumn (February-April) and two spring (September-November) germinations; *Chloris acicularis* and *C. truncata* — three autumn, three spring; *Digitaria coenicola* — three autumn, one spring. Rainfall immediately prior to germination was variable, but in all cases sufficient to moisten the soils to a minimum depth of 6 in. Air and soil temperature ranges were comparatively restricted for all species except *C. truncata,* and the lowest temperatures were associated with *S. falcata* (Table 6).

TABLE 6

TEMPERATURE AND RAINFALL RANGE DURING PERIODS OF VIGOROUS GERMINATION OF PERENNIAL GRASSES, 1948-52

Species	Mean Air Temperature (°F)*	Mean Soil Temperature at 1-in. Depth (°F)†	Rainfall (in.)
Stipa falcata	50-57	54-63 (12°-17°C)	0.80-1.40
Chloris acicularis and *Digitaria coenicola*	66-70	73-83 (23°-28°C)	0.90-9.00
Chloris truncata	57-75	62-90 (17°-32°C)	0.80-7.20

* (Mean maximum + mean minimum)/2.

† Calculated from mean air temperature.

Plant establishment from seedlings was generally weak and infrequent in all species. Seedlings of all species from at least one-third of the seasonal germinations listed above subsequently perished. *C. truncata* proved the poorest contributor of new plants to the community. Pantograph charting during the favourable period of March 1948-50 showed that *C. acicularis* clearly surpassed the other grasses (Fig. 4) in percentage survival of seedlings within an originally dense population (26 seedlings of all four species per sq. m.). In the same interval *S. falcata* established an equal number of new adult plants from a greater population of seedlings present at the outset.

Pantograph measurement of plant development was first taken for the period March 1948-50, in which rainfall was 18.5 in. for the first year and 29.3 in. for the second. Flooding then caused a break in these records. Development of a smaller population was traced during the 1-yr period March 1951-52 (rainfall 11.7 in.). Species differences in degree of development or decline were particularly evident among the small plants (diameter 1-3 cm). *Chloris truncata* showed the highest proportional loss of small plants during both study periods (Fig. 5*A*), at the same time suffering a heavy mortality of all plants above 3 cm diameter. *Stipa falcata* plants of medium size (diameter 3.5-6.5 cm) showed light losses in 1948-50 which were increased in the drier second period. By contrast, all plants of the medium size-group in *Chloris acicularis* and *Digitaria coenicola* persisted during each period. No mortality occurred among large plants (diameter above 6.5 cm) of *S. falcata, C. acicularis,* or *D. coenicola.*

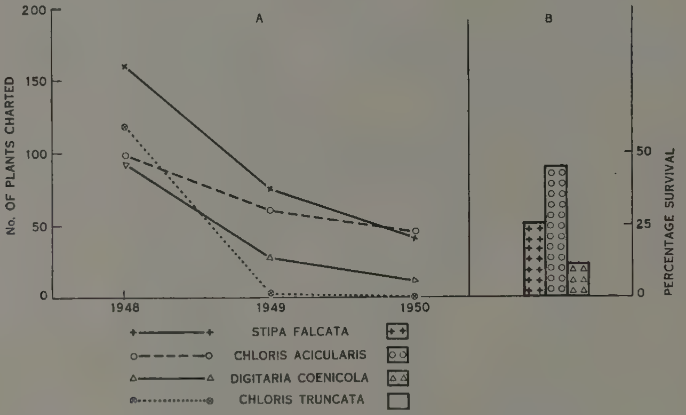


Fig. 4.—Seedling survival of perennial grasses from germination at March 1948, showing (*A*) changes in plant numbers (total population of each species from 18 pantograph quadrats) and (*B*) percentage survival at March 1950 in the same populations.

Considerable increases in mean basal area per plant were shown by small plants which persisted during March 1948-50 (Fig. 5*B*). The increases varied with species, being 7.7-, 6.5-, and 5.5-fold respectively for *D. coenicola, S. falcata,* and *C. acicularis.* In the same interval medium and large plants approximately doubled in size, the greatest proportional increase tending to occur with *C. acicularis.* During 1951-52 small and medium plants of *S. falcata* were considerably reduced in size, whereas all plants of *C. acicularis* and *D. coenicola* were relatively unchanged.

During the intervening period of March 1950-51 (rainfall 40.7 in.) an investigation was made of plant development in response to recurrent flooding over 8 months followed by a dry midsummer. *S. falcata* suffered serious mortality from the first flooding, even where submergence was shallow and relatively short-lived (Table 7). *C. acicularis* was the only species to display marked immunity to damage from deep flooding.

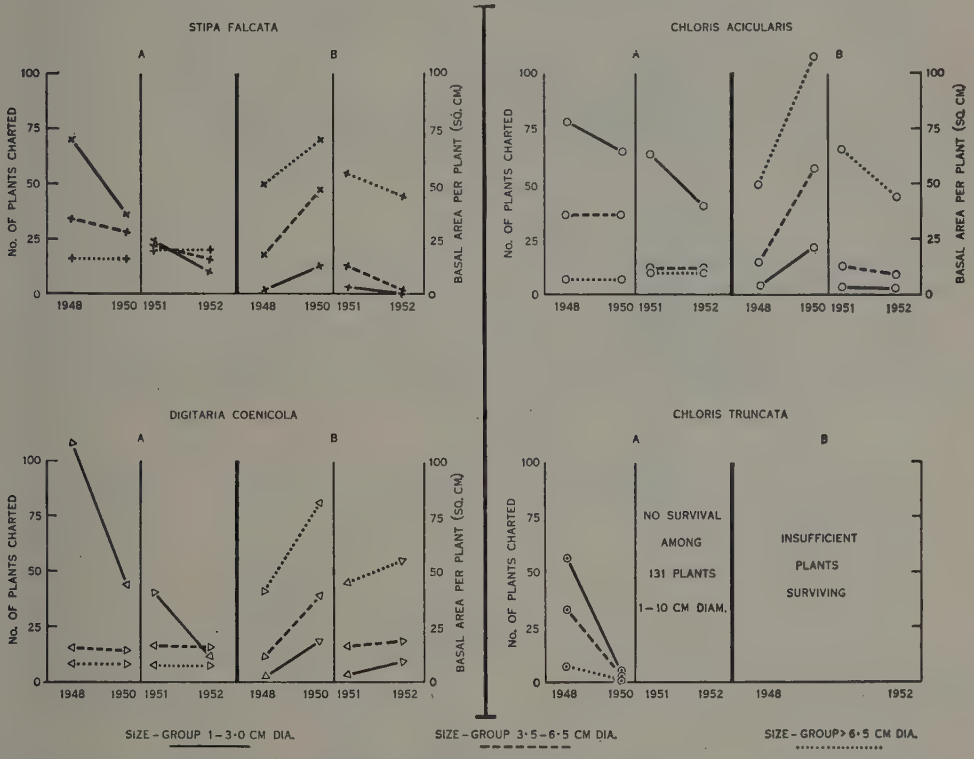


Fig. 5.—Development of established perennial grass plants of various size-groups during March 1948-50 and March 1951-52, showing changes in (*A*) plant numbers (from 12-18 pantograph quadrats) and (*B*) basal area of surviving plants (mean basal area per size-group expressed in sq. cm.).

Excessive rainfall in 1950 caused a distinct weakening of *S. falcata* on non-flood sites, surviving plants remaining weak over the summer (Fig. 6). *C. acicularis* in the same situations was relatively unchanged in basal area, and *D. coenicola* showed a marked increase. Recurrent deep flooding virtually eliminated the *S. falcata* population, while some plants of *C. acicularis* survived and apparently utilized the additional moisture for greater summer development.

Under the conditions of the experimental seasons (except 1950), the most vigorous plants of *S. falcata* and *D. coenicola* tended to reach a maximum basal diameter of 8-10 cm before apparent senility caused breaking of the tussocks. *C. acicularis* commonly attained a maximum of 11-12 cm, with isolated plants reaching 20-21 cm. The data on rates of development indicated that maximum plant size could be achieved by these species in a life span of 5-6 yr, given adequate rainfall and lenient grazing.

TABLE 7

EFFECT OF FLOODING ON PERENNIAL GRASSES, MAY 1950

Mean of 25 random quadrats

Species	Shallow Flooding			Deep Flooding		
	Unaffected* (%)	Partly Damaged* (%)	Killed* (%)	Unaffected (%)	Partly Damaged (%)	Killed (%)
Stipa falcata	21.5	14.2	64.3	—	6.7	93.3
Chloris acicularis	100	—	—	38.1	23.8	38.1
Digitaria coenicola	60.0	40.0	—	—	—	100
Chloris truncata	86.8	9.4	3.8	8.8	—	91.2

* Number of plants in each category expressed as a percentage of the total sample population of each species.

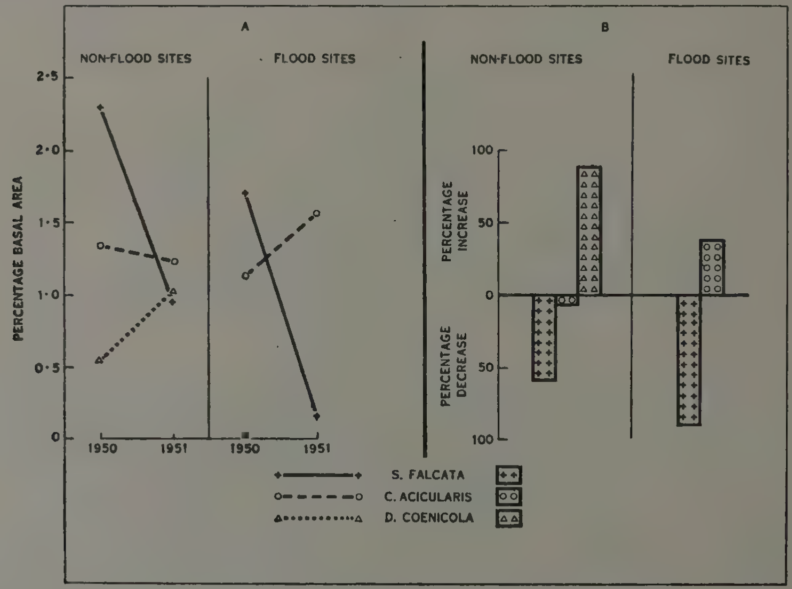


Fig. 6.—Development of three perennial grasses during March 1950-51, showing (*A*) changes in recorded basal area (mean of 32 permanent quadrats) and (*B*) percentage increase or decrease in basal area (1950-51 difference as a percentage of 1950 value). 'Deep-flood' sites (see Section II) and 'non-flood' sites are shown. The population of *D. coenicola* on the flood sites was insufficient for analysis.

C. truncata fell into a different category, rarely reaching a diameter of 10 cm and in the course of this study tending to die out after rapid growth (to 4-5 cm) occupying one favourable spring-summer-autumn period.

(*b*) *Seasonal Distribution of Production*

The four perennial grasses exhibited a similar distribution of green forage production during most years (Fig. 7); production rose from a midsummer minimum to a late summer (March) peak, declined to a midwinter trough, and rose again to a late spring (November) peak. The only departures from this general pattern were the midsummer peak at January 1951 (following a November rainfall of 9 in.) and the late summer minimum at March 1952 (following prolonged dry conditions). The January 1951 peak was, however, succeeded by a normal summer

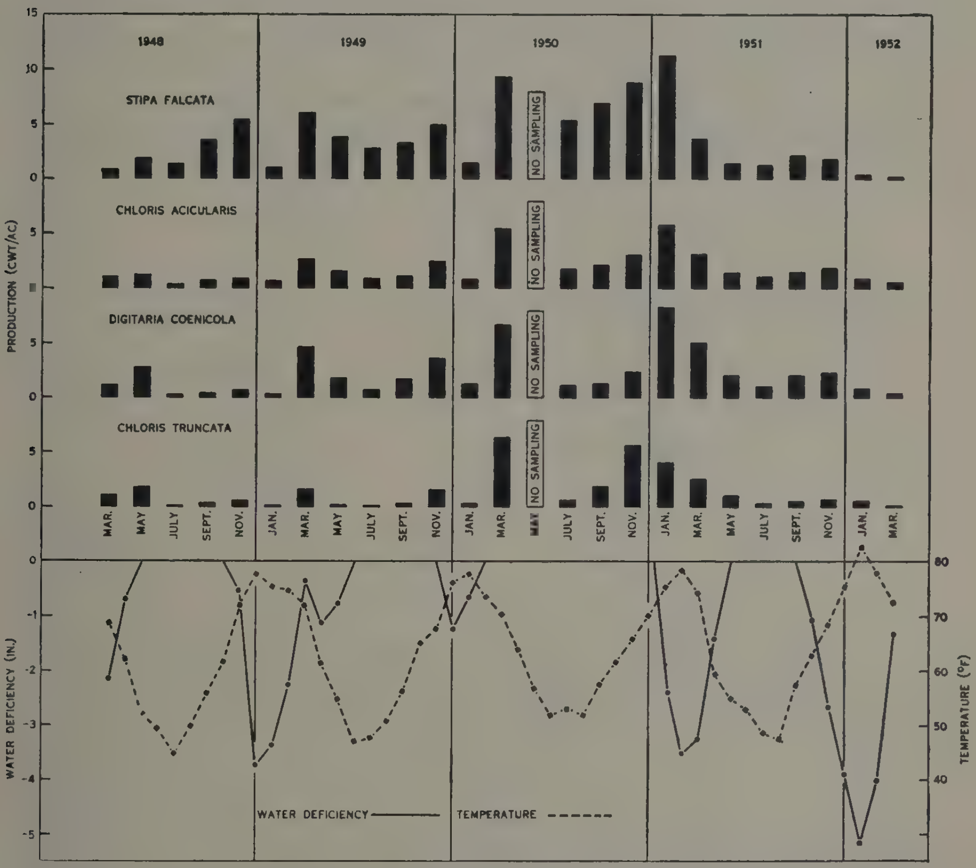


Fig. 7.—Seasonal production of four perennial grasses during March 1948-52 in relation to mean monthly water deficiency and temperature (production measured as the average quantity of green forage taken at bimonthly intervals from 8-32 random quadrats on the various sample areas). Water deficiency was determined from a comparison of rainfall and calculated potential evapotranspiration (Leeper 1950).

trough not shown in Figure 7 because of the length of the sampling interval. Normally, the March response tended to exceed the November response of all species; the reverse held only for *Stipa falcata* in 1948 when this species showed the greater susceptibility to the March water deficiency. *S. falcata* was also more affected than *Chloris acicularis* by the onset of dry conditions in early summer. In the November-January period *S. falcata* declined by 76 per cent. (mean of 1948, 1949, and 1951) as compared with a fall of 55 per cent. in *C. acicularis*.

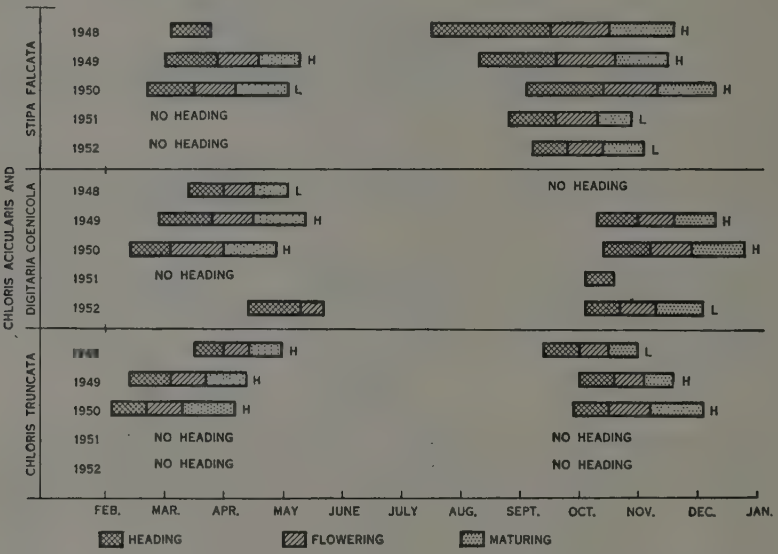


Fig. 8.—Phenological observations on perennial grasses, showing seasonal incidence of heading, flowering, and maturation periods, and relative magnitude of seed production. *H* = heavy seed production; *L* = light seed production.

While moisture was the limiting factor in most seasons, temperatures were sufficiently low in winter to inhibit production. *S. falcata* was least affected in this way, declining by only 25 per cent. (mean of 1948, 1949, and 1951) between May and July. The corresponding fall in *C. acicularis* was 42 per cent. and in *Digitaria coenicola* and *C. truncata* 75 per cent. Mean air temperatures in June and July of these years ranged between 48 and 53°F. In 1950 the temperature range associated with strong responses by all species was 70-73°F, excepting a lower level (62°F) which preceded the November peak in *C. truncata*. Lesser peaks in all species were preceded by mean temperatures as high as 79°F.

(*c*) *Phenology and Protein Content*

Life history studies over 5 yr showed that the species were capable of maturing in both late summer and spring of the one year (Fig. 8), given suitable moisture and temperature conditions. This was achieved by *Chloris truncata* in 1948, and by all four species in 1949 and 1950. Under the moist conditions of 1949 and 1950 *C. truncata* began flowering about mid February at 75°F, followed 2 wk later by *C. acicularis* and *Digitaria coenicola,* and then by *Stipa falcata* at mid March at 70°F. *Chloris* spp. and *D. coenicola* also began flowering at 62°F in 1948 when a dry interval delayed the stage until April.

S. falcata was invariably the first of the species to flower in spring; the stage usually commenced at mid September (56-58°F) but in 1950 was a month later. In 1949 and 1950 *C. truncata* began flowering by mid October (62-65°F), 1-2 wk ahead of *C. acicularis* and *D. coenicola.*

Heavy seed production in all species was confined to the first 3 yr (Fig. 8). During this period *C. truncata* and *S. falcata* were consistently strong seeders in autumn and spring respectively.

TABLE 8

CRUDE PROTEIN CONTENT OF PERENNIAL GRASSES AT VARIOUS GROWTH STAGES

Percentage N × 6.25

Species	Protein Percentage (whole plant)				
	Vegetative	Heading	Flowering	Seed Shedding	Dormant
Stipa falcata	10-11	11	10-12	6-9	6-7
Chloris acicularis	10-11	10-11	10-15	8-10	9
C. truncata	10-11	10-11	10-12	9	8-9
Digitaria coenicola	8-10	8-10	8-12	7-9	6-9

Each species showed only a small rise in crude protein content between the vegetative and flowering phases (Table 8). The sharpest decline between flowering and dormancy occurred in *Stipa falcata.* Lowest values were recorded in January (*S. falcata*) and July (*Chloris* spp. and *D. coenicola*).

(*d*) *Root Systems*

Root development of *Stipa falcata, Chloris acicularis,* and *Digitaria coenicola* growing on sandy soil (Fig. 9) was clearly differentiated into two systems. An upper dense mass was composed of multi-branched, thick main roots (most robust in *C. acicularis*), while a lower diffuse system was formed by thinner main roots sparsely branched but with copious root hairs. This characteristic was well illustrated by the high percentage of total root weight occurring in the top 6 in. (Fig. 9). Differences between species rested principally in the limits of horizontal and vertical penetration. In adult plants of equal basal diameter, radial spread of superficial roots was 4-5 in. greater in *C. acicularis* and *D. coenicola* than in *S. falcata.* Superiority in lateral extension was maintained to a depth of

36 in., since *Stipa* roots also showed relatively weak penetration of the clay layer below 24 in. *C. acicularis* possessed numerous strong main roots to 42 in., and below this level a sparse network of thin branch roots to 48 in. Development of *D. coenicola* in these deeper zones was restricted to a few thin, sparsely branched main roots.

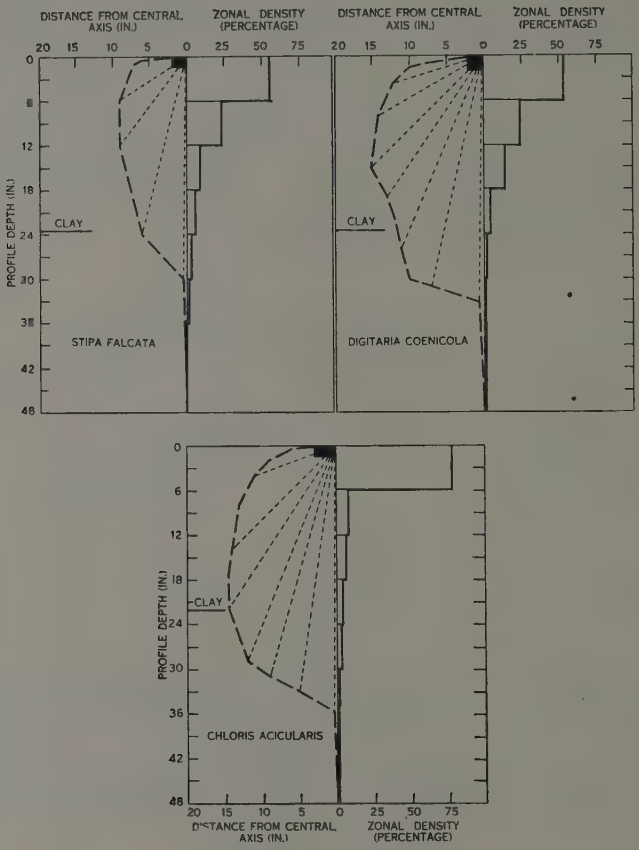


Fig. 9.—Diagram of characteristic root systems of three perennial grasses, showing extent of vertical penetration and lateral spread from central plant axis (left-hand side), and vertical distribution of root mass in 6-in. zones to a depth of 36 in. (weight of roots in each zone expressed as a percentage of the total root weight).

VI. Autecology of Winter Annual Species

(*a*) *Germination and Seedling Survival*

Medicago seed set mainly in October 1947 continued to produce crops of seedlings on all soil types during four subsequent seasons, although germination was weak after the second season (Fig. 10).

Germination of *Medicago* spp. could occur at any time between March and September (Fig. 11*A*); in addition, weak germinations were observed at mid February of 1949 and 1951. The most vigorous germinations were recorded in March, April, June, and July of different years, depending mainly on the amount and incidence of rainfall. Associated air and soil temperatures therefore showed a relatively wide range (Table 9). Germination in May and June was frequent in the years 1949 to 1952, and formed a considerable proportion of the total germination in these years (Fig. 11*B*). Soil temperatures of 51-61°F (at 1-in. depth) in May and June were therefore considered the more favourable for germination of *Medicago* spp.

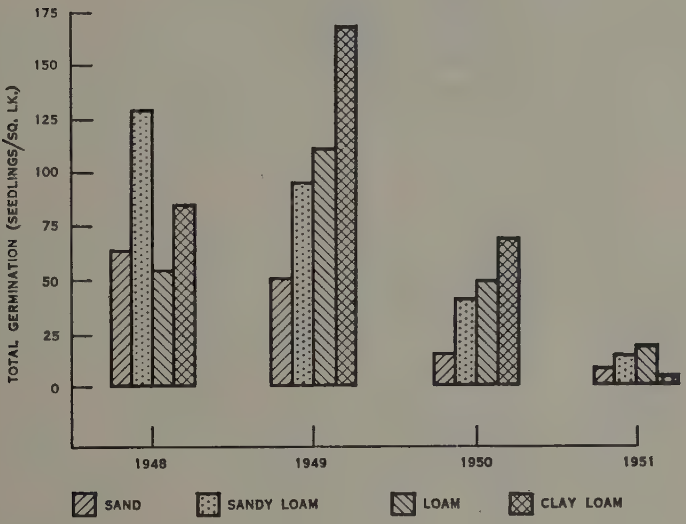


Fig. 10.—Germination of *Medicago* seed (set in 1947) over four subsequent years on four soil types (mean of two sites on each soil).

Erodium cygnorum and *Hordeum leporinum* germinated at mid February of all years except 1952. Germination was also successful in March, April, or May of various years, but was negligible in later months. Associated temperatures tended to be higher than those for *Medicago* spp. (Table 9); the most frequent soil temperature level within a wide tolerance range was 65-75°F. A laboratory test of *E. cygnorum* and *H. leporinum* seeds on moist filter paper indicated that 85°F marked the upper limit for germination.

Observations over the whole pasture showed that seedling persistency of *Erodium* and *Hordeum* surpassed that of *Medicago* spp. during temporary periods of moisture deficiency early in autumn, although in 1951 all seedlings from the February germination failed in April. During 1952

Medicago spp. and *Erodium* germinated together in April and May, and with adequate moisture the percentage seedling survivals of these species were similar at mid September on both sand and loam soil (Table 10).

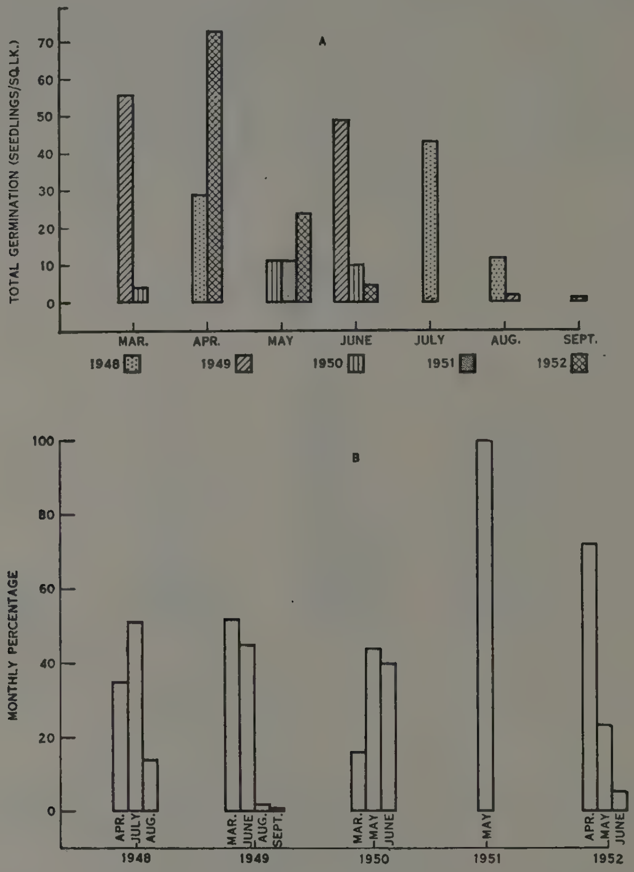


Fig. 11.—Seasonal incidence of germination in *Medicago* spp., 1948-52, showing (*A*) number of seedlings per sq. lk. (mean of all soils) and (*B*) monthly germination expressed as a percentage of the total germination in individual years.

(*b*) *Seasonal Distribution of Production*

Average production trends of *Medicago* spp. (principally *M. minima* in the sample population) and *Erodium cygnorum* showed a more or less exponential increase from May to September for 1948-49 (Fig. 12). *E. cygnorum* from February germination gave small but measurable responses in March and May, whereas *Medicago* spp. from March-April germination were negligible in development prior to mid May. *E. cygnorum* grew vigorously in March of the flood year (1950), and in November showed strong leaf regeneration on plants which had matured 1 month previously. Development of *Medicago* spp. in 1950 and 1951, and *E. cygnorum* in 1951 was virtually confined to July to September.

TABLE 9

RAINFALL AND TEMPERATURE RANGE DURING PERIODS OF VIGOROUS GERMINATION OF WINTER ANNUALS, 1948-52

Species	Mean Air Temperature* (°F)	Mean Soil Temperature at 1-in. Depth† (°F)	Rainfall (in.)
Medicago spp.	45-63	48-74 (9°-23°C)	0.69-7.19
Erodium cygnorum and *Hordeum leporinum*	55-70	60-80 (16°-27°C)	1.17-5.81

* (Mean maximum + mean minimum)/2.
† Calculated from mean air temperature.

Year to year variation occurred in the level of September production of the annual species, despite a sufficiency of moisture in the growing period beyond April (Table 11). September production of *Medicago* spp. and *Erodium* for the years 1948-52 was therefore plotted against March and April moisture deficiencies (Fig. 13). Regression coefficients of September production on April moisture deficiency were the only significant values ($P < 5$ per cent.)

TABLE 10

SEEDLING SURVIVAL OF MEDICAGO SPP. AND ERODIUM CYGNORUM ON SAND AND LOAM SOILS, 1952

	Sand		Loam	
	Medicago spp.	*E. cygnorum*	*Medicago* spp.	*E. cygnorum*
Total established seedlings from autumn-winter germinations*	1131	61	435	235
Total seedlings surviving at mid September*	366	24	121	62
Percentage survival	32.4	39.3	27.8	26.4

* Number of plants counted on 12 1-lk squares (mean of two sites on each soil).

(*c*) *Phenology and Protein Content*

Flowering of *Medicago* spp. generally commenced during August (Fig. 14), the incidence within the month largely depending upon the time of maximum germination and the winter growth rate. Under the sustained wet conditions of 1950, the onset of flowering was delayed until mid September. *Medicago minima* was always the first species of the group to begin flowering, followed at approximately weekly intervals by *M. laciniata* and then *M. hispida* var. *denticulata*. Flowering was usually completed in 1 month. First flowering of *Erodium cygnorum* was common late in July,

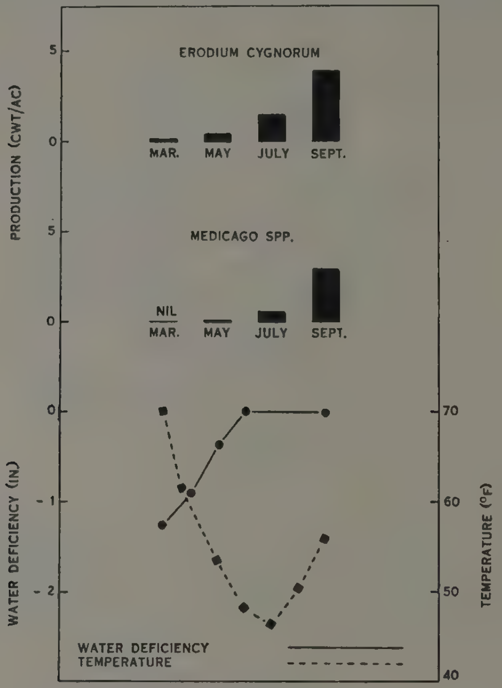


Fig. 12.—Average seasonal production of *Erodium cygnorum* and *Medicago* spp. for 1948-49 (production measurement as for perennial grasses).

TABLE 11

MONTHLY WATER DEFICIENCIES AT TRANGIE AGRICULTURAL EXPERIMENT STATION, MARCH TO SEPTEMBER 1948-52

Year	Water Deficiency* (in.)						
	Mar.	Apr.	May	June	July	Aug.	Sept.
1948	2.2	0.7	0	0	0	0	0
1949	0.3	1.1	0.8	0	0	0	0
1950	0	0	0	0	0	0	0
1951	3.2	1.4	0	0	0	0	0
1952	1.3	0	0	0	0	0	0

* Determined from a comparison of rainfall and calculated potential evapotranspiration (Leeper 1950).

while *Hordeum leporinum* flowered most frequently between mid August and mid September. With a few exceptions, e.g. *Medicago* spp. in 1950 and 1951, all species had matured by the third week of October. The ripening stage was extremely rapid in some years, occupying only about 2 wk under the influence of strong, hot winds.

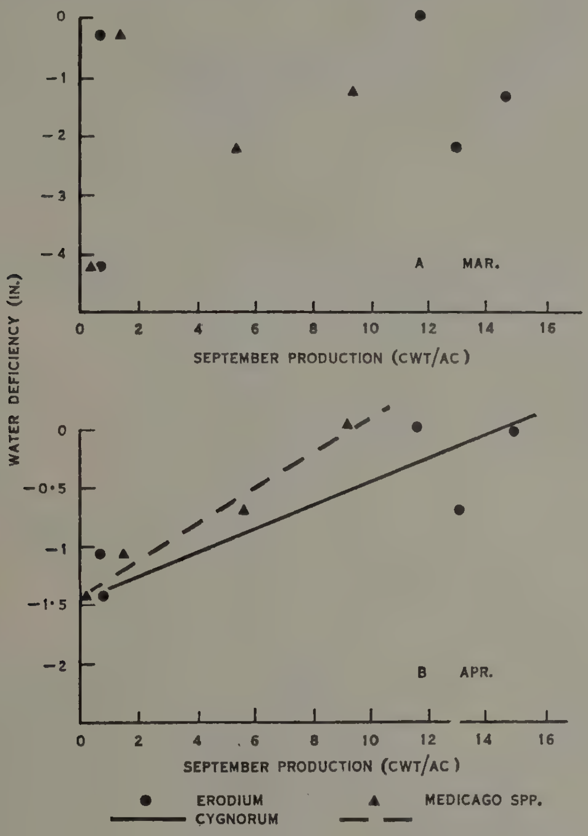


Fig. 13.—September production of *E. cygnorum* and *Medicago* spp. on sandy loam and loam soils 1948-52 in relation to water deficiency in (*A*) March and (*B*) April. Regression lines of the species are superimposed on the April graph.

Medicago spp. contributed a heavy seed production only in the first and last years of observation (Fig. 14). *E. cygnorum* invariably yielded an abundant seed crop, while seeding of *H. leporinum* was heavy in all years except 1951.

Medicago spp. and *E. cygnorum* showed a rise in crude protein content between the early vegetative and pre-flowering stages (Table 12). The legumes (including ripening burr) maintained a relatively high value after flowering, whereas a marked decline occurred in *E. cygnorum* and *H. leporinum*.

(*d*) *Root Systems*

The root system of adult *Medicago* plants on sandy soil was characterized by a taproot with a dense network of hard, scaly branch roots in the top 12 in. Lateral spread in this zone did not exceed 3-4 in., and the limit of vertical penetration was about 30 in. (Fig. 15). A distinct weakening of the system occurred at the top of the clay horizon, where the taproot divided into several thin, soft roots carrying only a few short branch roots. *Erodium cygnorum* possessed a thick, fleshy taproot in the upper 6 in. of the profile, with strong branch roots extending laterally for 5-7 in. Shorter branch roots were numerous in the 6-24-in. zone. At levels below 18 in. the taproot was protected by a fibrous sheath, and a weak penetrative power was indicated by a characteristic looping of the root above the clay

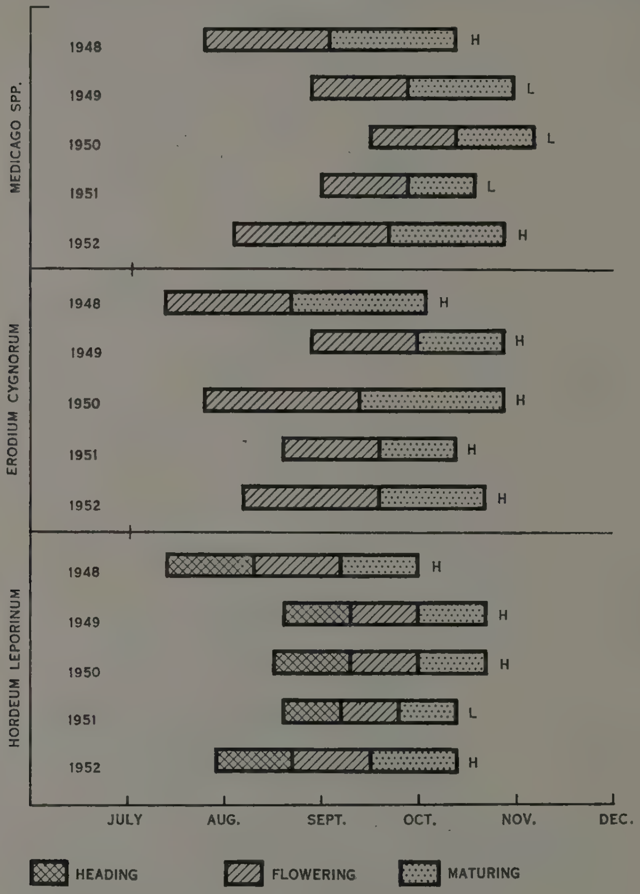


Fig. 14.—Phenological observations on winter annual species, showing incidence of flowering periods and relative seed production. *H* = heavy seed production; *L* = light seed production.

horizon. The root finally divided, sending several small branches along the top of the clay layer. A few fine roots from these horizontal branches were found to penetrate to 34 in. Lateral and vertical limits of the fibrous rooting system of *Hordeum leporinum* in a clay loam soil were similar to the above spatial limits in *Medicago* spp.

The root mass of all species was concentrated mainly in the top 6 in. of the profile (Fig. 15). Decline in root density between the 6- and 18-in. levels was least severe in *H. leporinum* and *Medicago minima.* Root density in *E. cygnorum* tended to be greater at 18-24 than at 12-18 in., owing to the looping of the taproot; only trace amounts could be extracted from lower levels.

TABLE 12

CRUDE PROTEIN CONTENT OF WINTER ANNUALS AT VARIOUS GROWTH STAGES
Percentage N × 6.25

Species	Protein Percentage (whole plant)		
	Early Vegetative	Pre-flowering	Post-flowering and Maturing
Medicago spp.	16	19-24	17-18
Erodium cygnorum	15	17-23	9-11
Hordeum leporinum	14-15	12-14	8-10

VII. DISCUSSION AND CONCLUSIONS

The perennial grasses were acutely sensitive to climatic fluctuations within both the moist years (1948-1950) and the drier years (1951-52). This susceptibility was strongly evident from the seasonal variation in incidence and magnitude of germination. Moisture availability was considered to be the principal limiting factor in this regard, but soil temperature was also operative in that all species except *Chloris truncata* tolerated only a narrow range for successful germination. Variable production of infertile or dormant seed may also have affected germination. This is suggested by reports from Breakwell (1920), Osborn, Wood, and Paltridge (1931), and Amy Myers and Neal-Smith (personal communications) on the difficulty of securing laboratory germination of *Stipa* spp., *Chloris* spp., and other native grasses of western New South Wales.

During the wet period of March 1948-50, established plants of all the perennial species suffered a high percentage mortality among the smaller plants, and yet sustained (except in *C. truncata*) a striking increase in development of the small plants which persisted. This feature, supported by the evidence of strong persistency of large plants (again excepting *C. truncata*) over the same period, indicated a close approach to the maximum population of perennial grasses tenable on the area. Support for this conclusion is also found in the general increase in percentage mortality during the drier period of 1951-52, and to some extent in the low rate of seedling survival throughout the study period. *C. acicularis* was shown to be the most stable species, and *C. truncata* the most variable species in plant development during the experimental period as a whole. *C. truncata* is usually regarded as a perennial species (Turner 1895; Breakwell 1920; Key 1945; Beadle 1948), but behaved as an annual species during this study.

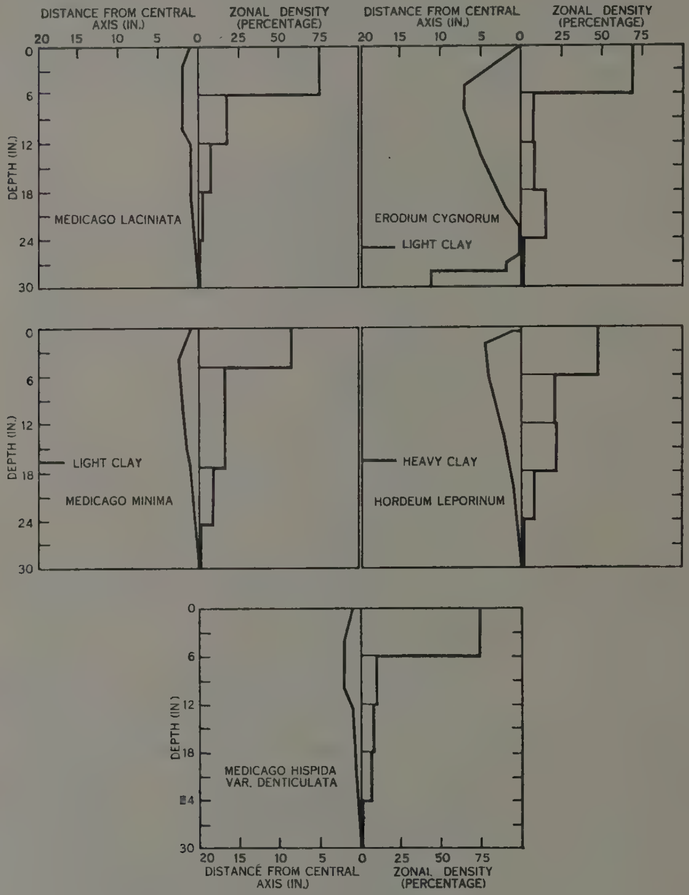


Fig. 15.—Diagram of characteristic root systems of five winter annual species, showing extent of root penetration (left-hand side), and root density (percentage of total root weight) in 6-in. zones to a depth of 30 in.

Rainfall was undoubtedly the principal factor controlling seasonal production of green forage by the perennial grasses. Temperature became limiting only in midwinter (June-July). The usual cycle of production for each species consequently took the form: late summer maximum — winter trough — spring peak — midsummer minimum. From the production aspect *Stipa falcata* was the species least depressed by midwinter temperatures, but was more sensitive than *Chloris acicularis* to summer moisture deficiency.

Strong superficial root systems in *S. falcata, C. acicularis,* and *Digitaria coenicola* permitted a rapid and efficient utilization of moisture derived from light rains of the respective growing seasons. In *S. falcata* the lack of an active absorption system below 18 in. was one factor inducing the marked summer decline in production of this species. *D. coenicola,* with a stronger absorption zone between 18 and 24 in., was better adapted than *S. falcata* to exploit the full depth of moisture penetration commonly found in sandy soil after late summer rains (Hutchings, unpublished data). *C. acicularis* possessed the strongest root system below 24 in., and thereby showed to advantage in withstanding prolonged dry conditions. Since roots are the principal organs in perennial grasses for storage of nutrient reserves (Weinmann 1948), it is likely that *C. acicularis* also derived the greater drought resistance by virtue of greater density and thickness of the main roots.

In addition to the adequate winter rainfall, three factors assured a regular recurrence of the annual species as an important winter component of the pasture. Firstly, all species were characterized by a free-seeding habit, even when ripening was hastened by the onset of hot, dry conditions in early spring. The presence of hard seed in *Medicago* spp., shown to be viable for several years in the field, also mitigated against failure of seed supply. In this regard, Ewart (1908) has recorded germination of *Medicago hispida* var. *denticulata* from seed as much as 17 yr old.

Secondly, all annual species were capable of germinating within a wide soil temperature range (48-80°F), so that effective rainfall received at any time between mid February and the end of May (or later in *Medicago* spp.) could produce a successful germination. The temperatures conformed to the range recorded by Trumble (1937) for maximum germination of winter annuals in South Australia.

The third perpetuating factor was the rapid growth rate of the species, particularly after mid July. Seedlings established as late as June were thereby capable of reaching maturity prior to the advent of dry summer conditions.

Conditions favourable to the development of highest September production of the annual species were more critical. In the presence of adequate moisture between May and September, maximum September production depended upon an adequate moisture supply in April. This finding compared with the report by Trumble and Cornish (1936) that rainfall in the autumn months, especially May, greatly modified final production of winter annuals under South Australian conditions. At Trangie the highest September production (in 1952) of *Medicago* spp. and *Erodium cygnorum* resulted from a late March germination of both species, followed by 2.7 in. of rain in April. Field observations suggested that higher temperatures and shading by maturing perennial grasses were other factors contributing to weak initial development of the annuals when germination occurred before mid March.

Extremely high densities (up to 100 plants per sq. lk.) were apparent in most early winter stands of *Medicago* spp. and *E. cygnorum*, so that a moderate density was maintained despite a seedling survival rate of only 30 per cent. (as in 1952). It seems likely that a density decline of this order would not have depressed the final production, since Donald (1951) has found that final production of dry matter from annual pasture plants was constant over a wide range of population densities.

Over the pasture as a whole, *E. cygnorum* proved more productive than *Medicago* spp. during the 5 yr of study. One operative factor in this regard was the superiority of *E. cygnorum* as a competitor for light in mixed populations of the annuals. This species was invariably taller than *Medicago* spp. during the major part of the growing season, and achieved a foliage canopy sufficiently dense to shade the lower strata.

While superficial root development (0-6 in.) was strong in all the annual species, *Medicago minima* and *Erodium cygnorum* appeared the best adapted to exploitation of the clay at lower levels. This feature was reflected in the suitability of all soils for the two species, and also in the lower susceptibility to wilting at times of temporary moisture stress.

It is clear from the production data for the favourable years of 1948 and 1949 (Figs. 7 and 12) that the winter annuals achieved vigorous development in association with a relatively dense stand of perennial grasses. The composite pasture therefore tended to show a September maximum rather than a March maximum in green forage production, with annual species predominant at the former peak and perennial species at the latter. It is hoped that further information on the relationship between the perennial and annual components will be forthcoming when the grazing experiment on the area has been completed.

The present study serves to emphasize the varying development and adaptability of the species in response to changes in seasonal moisture and temperature levels. If some or all of the important grasses, namely *Stipa falcata, Chloris acicularis, C. truncata,* and *Digitaria coenicola* are to be strengthened under grazing in many pastures of the Trangie district, then application of the closer knowledge of seasonal behaviour of the species should prove a valuable aid.

VIII. ACKNOWLEDGMENTS

The authors wish to thank Mr. J. N. Whittet, formerly of the Department of Agriculture, N.S.W., and Mr. C. M. Donald, of C.S.I.R.O., for their unfailing interest and encouragement during the course of the studies. Appreciation is expressed also to Mr. J. Tunny and Mr. B. E. Cameron, of C.S.I.R.O., and Mr. R. G. Lincoln, of the Department of Agriculture, for valuable assistance with field work and maintenance of research records. Finally, the authors are grateful to the Department of Agriculture for many facilities provided through the Manager of Trangie Agricultural Experiment Station.

IX. References

Beadle, N. C. W. (1948).—"The Vegetation and Pastures of Western New South Wales." (Govt. Printer: Sydney.)

Biddiscombe, E. F. (1953).—A survey of the natural pastures of the Trangie district, New South Wales, with particular reference to the grazing factor. *Aust. J. Agric. Res.* 4 (1): 1-28.

Black, J. M. (1943).—"Flora of South Australia." Pt. I. 2nd Ed. (Govt. Printer: Adelaide.)

Breakwell, E. (1920).—Popular descriptions of grasses. *Agric. Gaz. N.S.W.* **31**: 309-14.

Breakwell, E. (1921).—Popular descriptions of grasses. *Agric. Gaz. N.S.W.* **32**: 537-42.

Breakwell, E. (1923).—"The Grasses and Fodder Plants of New South Wales." (Govt. Printer: Sydney.)

Clark, L. R. (1947*a*).—An ecological study of the Australian plague locust (*Chortoicetes terminifera* Walk.) in the Bogan-Macquarie outbreak area, N.S.W. Coun. Sci. Industr. Res. Aust. Bull. No. 226.

Clark, L. R. (1947*b*).—Ecological observations on the small plague grasshopper, *Austroicetes cruciata* (Sauss.), in the Trangie district, Central Western New South Wales. Coun. Sci. Industr. Res. Aust. Bull. No. 228.

Clark, L. R. (1948).—Observations on the plant communities at "Bundemar", Trangie district, New South Wales, in relation to *Chortoicetes terminifera* (Walk.) and *Austroicetes cruciata* (Sauss.). Coun. Sci. Industr. Res. Aust. Bull. No. 236.

Cuthbertson, E. G. (1952).—Some rainfall characteristics at Trangie Agricultural Experiment Station. *J. Aust. Inst. Agric. Sci.* **18**: 19-21.

Donald, C. M. (1951).—Competition among pasture plants. I. Intraspecific competition among annual pasture plants. *Aust. J. Agric. Res.* **2** (4): 355-76.

Downes, R. G. (1947).—Soil survey of paddock 5*A*, Trangie Agricultural Experiment Station. Coun. Sci. Industr. Res. Aust. — Div. of Soils — Div. Rep. 8/47.

Ewart, A. J. (1908).—On the longevity of seeds. *Trans. Roy. Soc. Vict.* **21**: 1-203.

Hanson, H. C., and Love, L. D. (1930).—Comparison of methods of quadratting. *Ecology* **11**: 736-48.

Key, K. H. L. (1945).—The general ecological characteristics of the outbreak areas and outbreak years of the Australian plague locust (*Chortoicetes terminifera* Walk.). Coun. Sci. Industr. Res. Aust. Bull. No. 186.

Leeper, G. W. (1950).—Thornthwaite's climatic formula. *J. Aust. Inst. Agric. Sci.* **16**: 2-6.

Loewe, F. (1948).—Variability and periodicity of meteorological elements in the southern hemisphere with particular reference to Australia. I. Some considerations regarding the variability of annual rainfall in Australia. Commonw. Met. Bur. Aust. Bull. No. 39.

Maiden, J. H. (1889).—"The Useful Native Plants of Australia." (Govt. Printer: Sydney.)

Moore, C. W. E. (1953).—The vegetation of the south-eastern Riverina, New South Wales. II. The disclimax communities. *Aust. J. Bot.* 1 (3): 548-67.

Osborn, T. G. B., Wood, J. G., and Paltridge, T. B. (1931).—On the autecology of *Stipa nitida*. A study of a fodder grass in arid Australia. *Proc. Linn. Soc. N.S.W.* **56** (4): 299-324.

Stoeckeler, J. H., and Kluender, W. A. (1938).—The hydraulic method of excavating the root systems of plants. *Ecology* **19**: 355-69.

Thornthwaite, C. W. (1948).—An approach towards a rational classification of climate. *Geogr. Rev.* **38** (1): 55-94.

Trumble, H. C. (1937).—Some factors affecting the germination and growth of herbage plants in South Australia. *J. Dep. Agric. S. Aust.* **40**: 779-86.

Trumble, H. C., and Cornish, E. A. (1936).—The influence of rainfall on the yield of natural pasture. *J. Coun. Sci. Industr. Res. Aust.* **9**: 19-28.

Turner, F. (1895).—"Australian Grasses." Vol. 1. (Govt. Printer: Sydney.)

Upchurch, R. P. (1951).—The use of the trench-wash and soil-elution methods for studying alfalfa roots. *Agron. J.* **43**: 552-5.

Weinmann, H. (1948).—Underground development and reserves of grasses. *J. Brit. Grassland Soc.* **3**: 115-40.

BOTANICAL CONTRIBUTIONS OF THE NORTHERN AUSTRALIA REGIONAL SURVEY

II. STUDIES ON MISCELLANEOUS NORTHERN AUSTRALIAN PLANTS

By S. T. Blake*

(*Manuscript received May 1, 1953*)

Contents

	Page
Summary	99
Introduction	100
Families in alphabetical sequence	101
Index to families and genera	139

Summary

This is an account of portion of the botanical collections of the Northern Australia Regional Survey, 1946-47, chiefly from the Darwin-Katherine area. Families fully considered are Anacardiaceae, Aquifoliaceae, Araceae, Barringtoniaceae, Burseraceae, Casuarinaceae, Cochlospermaceae, Lauraceae, Leguminosae-Caesalpinioideae, Leguminosae-Mimosoideae (except *Acacia*), Meliaceae, Myristicaceae, Nymphaeaceae, Palmae, Pandanaceae, Passifloraceae, Pittosporaceae, Rhamnaceae, Rhizophoraceae, Rutaceae, Sapindaceae, Sonneratiaceae, and Sphenocleaceae. A few species of the following families are also discussed: Combretaceae, Cyperaceae, Euphorbiaceae, Gramineae, Leguminosae-Papilionatae, and Moraceae. In addition to discussions on taxonomy, synonymy, and orthography of names, the following additions to the flora of the Northern Territory are recorded: new species: *Dendrolobium stipatum, Desmodium polyneurum, Horsfieldia australiana, Sclerandrium grandiflorum*, and *Vavaea australiana;* species not previously recorded from Australia: *Mimosa acanthocarpa, Pistia stratiotes*, and *Sphenoclea zeylanica;* species already known from other parts of Australia: *Albizia canescens, Casuarina cunninghamiana, Colubrina asiatica, Cryptocarya cunninghamii, Cyperus platystylis, Cyperus ramosii, Hymenachne amplexicaulis, Neptunia gracilis, Passiflora foetida*, and *Petalostigma banksii.* Two new names are proposed, *Eulalia mackinlayi* (F. Muell.) S. T. Blake and *Terminalia ferdinandiana* Exell. The genera *Horsfieldia, Pistia, Sphenoclea*, and *Vavaea* have not previously been recorded from Australia and *Albizia, Colubrina, Cryptocarya, Dendrolobium, Hymenachne*, and *Mimosa* have not previously been recorded from the Northern Territory. *Sphenoclea* represents a new family (Sphenocleaceae) for Australia. *Cochlospermum fraseri, Cryptocarya cunninghamii*, and *Sphenoclea zeylanica* are also recorded for the first time from Queensland. The following reductions to synonymy are made: *Alectryon bleeseri* O. Schwartz to *Cupaniopsis anacardioides* (A. Rich.) Radlk.; *Barringtonia denticulata* (Miers) Knuth to *B. gracilis* (Miers) Knuth, which is treated as distinct from *B. acutangula* (L.) Gaertn.; *Buchanania oblongifolia* W. V. Fitzg. and *B. muelleri* Engl. var. *pilosa* Engl. to *B. obovata* Engl.; *Buchanania muelleri* Engl. to *B. arborescens* (Bl.) Bl.; *Ilex peduncularis* F. Muell. to *I. arnhemensis* (F. Muell.) Loes.; and *Pandanus delestangii* Martelli to *P. aquaticus* F. Muell.

---

* Queensland Herbarium, Brisbane, seconded as Botanist to the Northern Australia Regional Survey, 1946-47, by the Queensland Department of Agriculture and Stock.

INTRODUCTION

Between the middle of June and the end of October 1946, the Northern Australia Regional Survey of C.S.I.R.O. examined an area of about 27,000 sq. miles in the Katherine-Darwin area of the Northern Territory between 12° and 15° S. and west of 133° E. The scientific party of this first expedition consisted of Messrs. C. S. Christian (leader, C.S.I.R.O.), G. A. Stewart (pedologist, C.S.I.R.O.), L. C. Noakes (geologist, Bureau of Mineral Resources, Geology and Geophysics), and S. T. Blake (botanist, Queensland Herbarium, Brisbane). The collection of herbarium specimens approximated 1200 numbers, the majority of which consists of a minimum of six sheets. The time of the year was the middle and end of the dry season, which is very marked in this area. Most woody plants observed are represented in the collections (by flowering or fruiting specimens, or both), except some of the trees of the "jungles", but numerous herbaceous plants, especially annuals, were no longer in a suitable state for collecting; to some extent this gap was filled in April 1947 when a few days were spent at Katherine prior to a 6-wk traverse from Katherine to Lake Nash via Camooweal, Queensland, on the Survey's second expedition. While en route to Katherine in 1946, about 90 numbers were collected from the desert scrub in the neighbourhood of Tennant Creek and the hitherto unexplored country to the east.

The original plan had been to present a comprehensive account of these collections, but a prior task was the preparation with C. S. Christian of an account of the vegetation of the area for the "General Report on Survey of Katherine-Darwin Region, 1946" (C.S.I.R.O. Aust. Land. Res. Ser. No. 1). This demanded the immediate checking of all field determinations against the specimens collected, Ewart and Davies' *Flora of the Northern Territory* (Melbourne, 1917), and more recent publications. It was found that some common plants were not listed by Ewart and Davies, that some were undescribed, and that some nomenclatural adjustments were necessary. These circumstances alone, apart from the time necessary to work up the whole of the collections and pressure of other work, made necessary a modification of the original plan. Two papers were prepared dealing with groups containing species of which the names appear in the *Report* but which are either not listed by Ewart and Davies or else listed under erroneous names. The first deals with *Eucalyptus*, of which a revision of the species in the area was found necessary (Aust. J. Bot. 1 (2): 185-352). The present paper deals with the remaining species and their names; where practicable, the families containing these species have been treated and opportunity was taken to include some other families of which few specimens were collected and in which any taxonomic and nomenclatural difficulties appear to have been removed. The families dealt with are listed in the Summary; 69 species are involved. Five new species are described and one new name and one new combination proposed. In all, 18 species are recorded from the Northern Territory for the first time; two of the previously described ones are also new for Queensland and two new for Australia. One family is recorded as new for Australia (Northern Territory and Queensland). Six names are treated as new synonyms; several adjustments to previously accepted nomenclature are made, none of which are new proposals, though some variations in orthography are discussed for the first time. Field characters of many species have not been described before; they are recorded here for all species, usually in the citation of specimens with other data on the labels, but are summarized in a subsequent paragraph when several collections are cited.

The only Flora dealing specifically with the Northern Territory is that by Ewart and Davies mentioned above. This was based on Bentham's "Flora Australiensis" (1863-78) and an annotated copy of F. Mueller's "Second Census of Australian Plants" (1889) referred to by Ewart and Davies as "National Herbarium Census". Many localities quoted are not in the Northern Territory and some of the records of species from the area thus have no foundation; on the other hand many species originally described from the area received only incidental mention. More extensive accounts of *Acacia* and *Eucalyptus* by J. H. Maiden and of the other capsular-fruited Myrtaceae by E. Cheel appear as Appendixes. Ewart and co-workers published further records in Proc. Roy. Soc. Vict.; Spencer Moore described several species in J. Linn. Soc. Lond. 45: 159-220 (1920); and in 1927, in *Repertorium Specierum novarum Regni Vegetabili* 24: 80-109, Otto Schwartz described many new species and published many new records from the neighbourhood of Darwin, chiefly from specimens collected by F. A. K. Bleeser.

In this series of papers, bibliographical references will usually be restricted to the place of the original description of the accepted name and synonyms, to "Flora Australiensis" (cited "Benth. op. cit.", except when it is the place of original publication or when other works of Bentham are also cited), "Flora of the Northern Territory" (cited "Ewart and Davies, loc. cit."), monographs, and first records of the species from the Northern Territory if not recorded in the "Flora of the Northern Territory". Monographic treatments of groups will be followed when practicable, but fresh revisions of some groups will be necessary. Photographs of herbarium specimens are the work of the Photographic Section, Department of Agriculture and Stock, Brisbane.

ANACARDIACEAE

Buchanania obovata Engl. in DC. Monogr. Phan. 4: 187 (1883)

B. muelleri Engl. var. *pilosa* Engl. op. cit. 190 (1883).

B. oblongifolia W. V. Fitzg. in J. Proc. Roy. Soc. W. Aust. 3: 166 (1918).

NORTHERN TERRITORY.—Near Brocks Creek, widespread and fairly common in open *Eucalyptus* forest, about 120 m, 13.vii.1946, *Blake* 16447 (deciduous tree, about 6 m high; grey, fissured, somewhat tessellately scaly bark, red when cut and exuding a resinous sap; light dull green, stiff leaves; green fruit)—*fruiting and leafy twigs, bark;*

near Ferguson R., NW. of Katherine, *Eucalyptus* forest on light grey podzol, alt. about 135 m, 24.vi.1946, *Blake* 16080*A* (tree, 9-12 m high; dark grey, rough, tessellated bark; open crown of deciduous subglaucous leaves; twigs with somewhat gummy sap; yellowish flowers)—*fl.*

A deciduous species rather widely spread in the region in *Eucalyptus* forest and allied communities, sometimes flowering when quite small. *B. obovata* was described from flowering material; portion of the type collection is in herb. Brisbane. *B. muelleri* var. *pilosa* was described from fruiting material; both syntypes are represented in herb. Brisbane. Type material of *B. oblongifolia* was seen in herb. Perth. The specimens referred to *B. latifolia* Roxb. by Fitzgerald (loc. cit.), and by Gardner (Enum. Pl. Austr. Occid. 74 (1930)), belong here, as do also some of the specimens referred to *B. angustifolia* Roxb. by Bentham (Fl. Aust. **1**: 490 (1863)).

Buchanania arborescens (Bl.) Bl. Mus. Bot. Lugd. Bat. **1**: 183 (1850); C. T. White, Proc. Roy. Soc. Qd. **61**: 56 (1950)

Coniogeton arborescens Bl. Bijdr. 1156 (1826).

? *Buchanania muelleri* Engl. in DC. Monogr. Phan. 4: 190 (1883), excl. var.

NORTHERN TERRITORY.—12° 43′ S., 131° 30′ E., patch of monsoon forest, 17.ix.1946, *Blake* 17039 (tree 12-15 m high; grey, very finely fissured bark, red immediately beneath surface, then striped red and whitish to the whitish sapwood; dark green leaves paler beneath; white flowers; immature fruit green)—*fl.*, immature *fr.*

A tree of the "jungles" (monsoon forests) and fringing forests. Australian specimens closely match Malaysian ones. *B. muelleri* Engl. appears to be based, at least in part, on specimens of this species (I have seen part of Daemel's collection from Cape York, which is a syntype) and partly perhaps on specimens of *B. obovata* with which the description of a shortly hairy fruit with an excentric apiculus is in better agreement (in *B. arborescens* the fruit is glabrous or nearly so and the apiculus is usually terminal, rarely slightly excentric). *B. muelleri* var. *pilosa* Engl. is certainly the same as *B. obovata.* In the original description Engler indicated that specimens of *B. muelleri* were referred by Bentham (Fl. Aust. **1**: 490 (1863)) to *B. angustifolia* Roxb. (a species with different stamens) and by Mueller (Fragm. 7: 23 (1869)) to *B. arborescens.* But one of the two collections cited by Mueller is the type of *B. obovata* Engl.

AQUIFOLIACEAE

Ilex arnhemensis (F. Muell.) Loes. in Engl. & Prantl, Nat. Pfl.fam. Nachtr. **1**: 218 (1897), and Nov. Act. Acad. Caes. Leop.-Carol. Nat. Cur. **78**: 68 (Monogr. Aquif. **1**: 68) (1901)

Byronia arnhemensis F. Muell. Fragm. **2**: 119 (1861); Benth. op. cit. **1**: 396 (1863); Ewart & Davies, loc. cit. 217.

Ilex peduncularis F. Muell. Fragm. **7**: 105 (1870), non Reissek (1861); *syn. nov.*

NORTHERN TERRITORY.—Near Mt. Finniss (12° 57′ S., 130° 47½′ E.), bank of One Mile Creek, in fringing forest, 90 m, 9.viii.1946, *Blake* 16740 (tree to 9 m high with transversely ridged, lenticellate, hard, pale grey bark; rather light green leaves paler beneath; whitish petals)—*fl., bark;* about S. of mouth of Daly R., 13° 45′ S., 130°

11′-15′ E., wet creek bank, 21 m, common, 24.vii.1946, *Blake* 16598 (tree to 9 m; pale green leaves; greenish buds)—*buds.*

A fairly common tree in the fringing forests in the NW. part of the Northern Territory; also in Western Australia and in similar habitats in northern Queensland.

As a genus, *Byronia* Endl. was distinguished from *Ilex* chiefly on the grounds that that there were at least twice as many ovary cells and stigmatic rays as sepals and petals. Later it was found that the number of ovary cells varied considerably in undoubted species of *Ilex,* and more recent students of the family have treated *Byronia* as a subgenus of *Ilex* (for example, Loesener in the works quoted above and S. Y. Hu in J. Arnold Arbor., particularly **31**: 214 (1950)). In 1901, Loesener (loc. cit. 220), stated that *I. peduncularis* F. Muell. was scarcely distinct from *I. arnhemensis;* from the material now available it seems indistinguishable. Both collections cited above carry male flowers only.

ARACEAE

Amorphophallus galbra F. M. Bail. Qd. Dep. Agric. Bot. Bull. **7**: 68 (1893); C. T. White, Proc. Roy. Soc. Qd. **61**: 55 (1950)

NORTHERN TERRITORY.—Cannon Hill, about 12° 24′ S., 132° 55′ E., in monsoon forest at base of cliffs, 2.x.1946, *Blake* 17115 (tuberous, leafless herb; scape erect, 60-120 cm high, pale grey mottled dark greenish; spathe greyish to yellowish, paler inside; spadix creamy)—*fl., fr.*

Previously known only from the type collection from the Barron River, Queensland, and Thomson's collection cited by White. The species is distinguished by its long, narrow spathe. Like other species of this genus, it produces leaves and flowers at different times of the year; one tuber produced two leaves in Brisbane in 1948. The specific epithet is the native name of the plant recorded by the original collector, and not a mistake for *glabra* as the compilers of *Index Kewensis* appear to have thought. The tubers are eaten by the natives in the country about Cannon Hill (Plate 1, Fig. 2).

Pistia stratiotes L. Sp. Pl. 963 (1753)

NORTHERN TERRITORY.—Near "Koolpinyah", 12° 26′ S., 131° 13′ E., covering surface of nearly dried-out lagoons and on mud at water's edge, 10.ix.1946, *Blake* 16966 (pale green rosettes; whitish inflorescence)—*fl.;* Daly R., about 13° 45′ S., 130° 42′ E., 12 m, free-floating pale green tufts on a lagoon, 19.vii.1946, *Blake* 16525—*sterile.*

New for Australia, though previously known from many places in the tropics generally. *Blake* 16525 was collected in the barren state because it was recognized as a new record for the continent, and it was not expected that flowering material would be found (Plate 1, Fig. 1).

BARRINGTONIACEAE

In most works on the Australian flora this group of genera has been placed under the Myrtaceae as tribe Lecythideae, subtribe Barringtoniae, or else treated with the Lecythidaceae. There seems good reason for treating the group as a separate family as was done by Miers and R. Knuth in their monographs of the group in Trans. Linn. Soc. (2) **1:** 47-118 (1875) and Pflanzenr. **105 (IV: 219)** (1939) respectively. Both Miers and Knuth have treated *Planchonia* Bl. as generically distinct from *Careya* Roxb., and this treatment is followed here. I have also followed Knuth in accepting *Barringtonia* J. R. & G. Forst. (*nom. conserv.*) in its traditional sense to include the Australian forms referred to *Stravadium* Juss. by Miers.

Barringtonia gracilis (Miers) R. Knuth, Pflanzenr. **105 (IV: 219)**: 44 (1939)

B. denticulata (Miers) R. Knuth, loc. cit.: *syn. nov.*

Stravadium gracile Miers, Trans. Linn. Soc. (2) 1: 86 (1875).

S. denticulatum Miers, loc. cit. 88.

NORTHERN TERRITORY.—About S. of "Koolpinyah", 12° 32′ S., 131° 14′ E., chiefly at the edge of channels and swamps, 10.ix.1946, *Blake* 16968—*fl.;* Daly R., about 13° 45′ S., 130° 42′ E., common around lagoons and subject to inundation for greater part of plant, 12 m, 19.vii.1946, *Blake* 16518—*fl., fr.;* Daly R., 13° 55′ S., 131° 12½′ E., in fringing forest, about 37 m, 2.vii.1946, *Blake* 16279—immature *fr.*, few old *fl.;* about 14° 7′ S., 131° 16-18′ E., about 45 m, edge of lagoon, 1.vii.1946, *Blake* 16264—old *fl.:* near Margaret R., in about 13° 6′ S., 131° 22′ E., hard grey soil, edge of lagoons, alt. about 25 m, 8.vii.1946, *Blake* 16394—*fl.*

Barringtonia gracilis is a small, crooked tree up to 9 m high, often with two or more trunks, with brown or greyish, fissured, sometimes somewhat scaly-looking bark, green leaves paler beneath, red flowers, and light green fruits. The trees grow along the margins of swamps, lagoons, and streams in the more northern parts of Australia; they are more or less completely inundated during the wet season and frequently quite leafless during the dry season. Flowering may commence on leafless branchlets or racemes may be found among leaves of varying age. Leaves on herbarium specimens accordingly show considerable variation in size and texture. The length of the pedicel varies considerably. The species is commonly known as "freshwater mangrove" or "itchy-tree", the itchiness produced by it probably being caused by the debris remaining on the trunk and branches from the previous flood (Plate 1, Fig. 4).

The Australian specimens have been very generally referred to *B. acutangula* (L.) Gaertn., but to judge from Gaertner's figure and Miers's elaborate description and detailed figures taken from the type specimen (Miers, loc. cit. 80 and pl. XVII, figs. 1-14, as *Stravadium acutangulum* (L.) Miers), and specimens from India in herb. Brisbane agreeing therewith, our tree differs in having shorter petioles, leaves less prominently toothed in the upper part and quite entire for a usually considerable distance above the base, usually longer (sometimes very long) but very slender pedicels, and perhaps in the greater tendency to produce prominently winged fruits. In *B. acutangula* the angles of the fruits are not (ever?) winged; in *B. gracilis* the fruits are usually prominently 4-winged. Knuth (loc. cit. 4) referred to *B. acutangula* one Australian specimen (*Bleeser* 80) which I have not seen; the others seen by him were referred to *B. coccinea* (Lour.) Kostel, a species based on a Loureiro specimen from Cochin-China now in the British Museum and described in some detail by Miers. The Australian specimens differ from those of *B. coccinea* in having generally longer pedicels, more nearly glabrous sepals, and 4-angled (not 8-angled) ovary and fruit.

I am indebted to the Director of the Royal Botanic Gardens, Kew, for a photograph of the type of *Stravadium denticulatum* Miers. The sheet bears 3 leaves, 2 detached, 1 attached to a short piece of stem, and a detached inflorescence; it was annotated by R. Knuth as "B. racemosa (L.) Bl.", though in his monograph Knuth implied that he did not see the specimen. Duplicate types of *Stravadium gracile* Miers are in Melbourne with sketches and fragments in Brisbane; Knuth also implied that he did not see specimens of this form, and his combinations appear to have been based on the descriptions of Miers alone. It is somewhat doubtful whether Knuth really intended to accord these forms specific status; the relevant passage follows immediately after his treatment of *B. coccinea* and reads "In den Formenkreis der Art gehören:

b. *B. denticulata* (Miers) R. Knuth n. comb. . . . . . .

c. *B. gracilis* (Miers) R. Knuth n. comb. . . . . . .".

To my mind, all the Australian specimens represent a single species, differing from both *B. acutangula* and *B. coccinea* as detailed above, and from *B. racemosa* (L.) Bl. in the very much smaller leaves and flowers, slender racemes, the 4 regular sepals distinct in bud, smaller more or less winged fruit, etc. *Stravadium gracile* and *Stravadium denticulatum* were published simultaneously. I have chosen the former epithet for the species because it was based on better material, though the dimensions of the sepals and petals are somewhat exaggerated in the original description.

Planchonia careya (F. Muell.) R. Knuth, Pflanzenr. **105** **(IV: 219)**: 56 **(1939)**

Planchonia crenata Miers, Trans. Linn. Soc. (2) 1: 91 (1875).

Barringtonia careya F. Muell. Fragm. 5: 183 (1866).

Careya australis F. Muell. Fragm. 5: 183 (1866) *pro syn.*, First Census Aust. Pl. 60 (1882); Ewart & Davies, loc. cit., 198.

Careya arborea Roxb. var. (?) *australis* Benth. Fl. Aust. 3: 289 (1867).

Cumbia australis (F. Muell.) Britten, J. Bot., Lond. 39: 68 (1901).

NORTHERN TERRITORY.—Mary R., about 13° 5′ S., 131° 47′ E., alluvial flats, about 60 m, 29.ix.1946, *Blake* 17089 (tree up to 7.5 m high; dark grey, coarsely longitudinally fissured, hard bark with occasional transverse furrows; pale green, more or less deciduous leaves; white flowers, the filaments pink at base)—*fl.*

One of the small deciduous trees rather widely distributed in the open forests of Northern Australia, extending south to about 23° S. in eastern Queensland.

BURSERACEAE

Canarium australianum F. Muell. Fragm. 3: 15 (1862); Benth. op. cit. **1**: 377 (1863); Ewart & Davies, loc. cit. 158

NORTHERN TERRITORY.—Daly R., Florina Crossing, 14° 26′ S., 131° 39′ E., fringing forest at top of bank, about 82 m, 25.x.1946, *Blake* 17302 (shapely tree about 10 m high; light grey, tessellated and coarsely scaly bark; deciduous green leaves paler beneath; purplish blue fruits)—*fr.*

Chiefly near river banks; also in Western Australia and Queensland. Apparently by a slip of the pen, Bentham (loc. cit.) wrote *australasicum* for the specific epithet, and this has been followed by some authors.

CASUARINACEAE

Casuarina cunninghamiana Miq. Revis. Casuar. 56, *t.* 6 (1848)

NORTHERN TERRITORY.—Daly R., about 14° 5′ S., 131° 15′ E., abundant in an open fringing forest, about 36 m, 1.vii.1946, *Blake* 16255 (tree, 15-18 m high; grey, closely fissured, roughened bark; dull green crown)—*fr.*

New for the Northern Territory; previously known from Queensland and New South Wales. A characteristic tree of river banks.

COCHLOSPERMACEAE

Cochlospermum fraseri Planch. Lond. J. Bot. **6**: 307 (1847); Benth. op. cit. **1**: 106 (1863)

C. heteronemum F. Muell. Kew J. Bot. 9: 15 (1857); Benth. op. cit. 1: 106 (1863).

Maximilianea fraseri (Planch.) O. Ktze. Rev. Gen. 1: 44 (1891); Ewart & Davies, loc. cit. 195.

M. heteronema (F. Muell.) O. Ktze. Rev. Gen. 1: 44 (1891); Ewart & Davies, loc. cit. 195.

NORTHERN TERRITORY.—Near Brocks Creek, gentle slope with grey podsol, "orchard country" dominated by dwarf trees of *Eucalyptus foelscheana* and *E. confertiflora*, alt. 92 m, 25.vi.1946, *Blake* 16110 (more or less erect tree 3-4.5 m high with rather smooth light grey bark; leaves deciduous, green to pale orange; flowers clear yellow)—*fl.* QUEENSLAND.—Burke district: Adel's Grove (NE. of Camooweal), rocky banks and ravine sides, 13.vii.1947, *de Lestang* 379 (tree 4.5-6 m, deciduous at flowering time; flowers clear yellow)—*fl.*

New for Queensland; widely spread in the northern part of the Northern Territory in open forest and particularly common on stony ground (Plate 1, Fig. 3); also in Western Australia. It flowers when nearly or quite leafless and is then a very showy plant.

In the account of the vegetation of the Katherine-Darwin Region (C.S.I.R.O. Aust. Land Res. Ser. No. 1 (1953)) this species was referred to *C. heteronemum*, but further studies with a wider range of material lead me to believe that the differences in indumentum on the inflorescence and the size of sepals supposed to distinguish this from *C. fraseri* are quite inconstant and that only one species is represented by the two names.

Most authors have followed Bentham's spelling of *heteroneurum*, but this is an evident misreading for *heteronemum* which refers to the difference in thickness of the filaments. *Cochlospermum* Kunth is conserved against *Maximilianea* Mart. (1819) non *Maximiliana* Mart. (1824?). Martius's name was spelt *Maximiliana* by O. Kuntze (loc. cit.) and *Maximilliana* by Ewart and Davies. Ewart and Davies also wrongly attributed the combination *M. fraseri* to Planchon and *M. heteronema* (*"heteroneurum"*) to F. Mueller.

Bentham and others referred the genus to Bixaceae.

COMBRETACEAE

Terminalia ferdinandiana Exell in herb. brisban., nomen novum

Terminalia edulis F. Muell. Fragm. 2: 151 (1861); Benth. op. cit. 2: 501 (1864); Ewart & Davies, loc. cit. 212; non Blanco, Fl. Filip. ed. 2: 265 (1845).

Some years ago, the specimens of *Terminalia* in the Queensland Herbarium were sent for examination to Mr. A. W. Exell at the British Museum. Exell noted that Mueller's name was a later homonym and wrote up the specimens as *T. ferdinandiana* Exell but never published the name.

Terminalia canescens (DC.) Radlk. in Th. Dur. Ind. Gen. Phan. 520 (1888), Sitzb. Akad. Muench. 20: 129 (1890) *in obs.;* non Engl. (1895)

Alectryon canescens DC. Prodr. 1: 617 (1824).

Terminalia circumalata F. Muell. Fragm. 3: 91 (1862); Benth. op. cit. 2: 499 (1864); Ewart & Davies, loc. cit. 212.

The family will be treated in more detail at a later date.

CYPERACEAE

This family was abundantly collected and will be discussed elsewhere; only two of the new records are reported here.

Cyperus ramosii Kükenth. Repert. Nov. Spec. Regn. Veg. 21: 326 (1925)

NORTHERN TERRITORY.—E. of Fog Bay, 12° 50′-51′ S., 130° 26′-27′ E., in patch of monsoon forest, shallow lateritic soil, 24 m, 12.viii.1946, *Blake* 16778 (spreading annual tufts — specimens dead).

New for the Northern Territory, where it was observed in a few of the "jungles" (patches of monsoon forest) in the general neighbourhood of Darwin; previously known from Queensland and the Philippine Is.

Cyperus platystylis R. Br. Prodr. 214 (1810)

NORTHERN TERRITORY.—E. of Fog Bay, 12° 50′-51′ S., 130° 30′-31′ E., on floating islands in large swamp about 9 m, 12.viii.1946, *Blake* 16788; Daly R., about 13° 45′ S., 130° 42′ E., in lagoon, submerged in about 70 cm of water, 12 m, 19.viii.1946, *Blake* 16521; 12° 55′ S., 132° 30′ E., edge of lagoon with *Hymenachne* and *Polygonum*, 17 m, 1.x.1946, *Blake* 17106; South Alligator R., 13° 5′ S., 132° 18′ E., forming floating islands on logs, etc., 30.ix.1946, *Blake* 17098.

New for the Northern Territory; previously known from eastern Australia through parts of Malaysia to India. It is one of the constituents of the floating islands met with in swamps, lagoons, and backwaters, forming green, erect tufts, 60-100 cm high with pale green to golden brown spikelets.

EUPHORBIACEAE

Petalostigma banksii Britten & S. Moore, J. Bot., Lond. 41: 225 (1903)

NORTHERN TERRITORY.—On Nutwood Downs Station, 16° 5′ S., 134° 26′ E., forming with *Eucalyptus* sp. a very open grassy forest, 201 m, 2.v.1947, *Blake* 17604 (tree of 4 m with ascending branches; bark dark grey, rough, and furrowed; leaves green to yellowish)—*fr.*

New for the Northern Territory; previously known only from Queensland. It is a small tree fairly common in places.

The family will be discussed at a later date.

GRAMINEAE

This family was abundantly collected and will be discussed elsewhere. One new species, one new combination, and one new record are treated here.

Hymenachne amplexicaulis (Rudge) Nees, Agrost. Bras. 276 (1829)

Panicum amplexicaule Rudge, Pl. Guian. 1: 27 (1805).

NORTHERN TERRITORY.—Near Cannon Hill, about 12° 24′ S., 132° 55′ E., in large swamp, forming large rich green masses, 2.x.1946, *Blake* 17141; E. of Fog Bay, 12° 50′-51′ S., 130° 36′-37′ E., drainage channel in seasonally swampy ground, 9 m, 10.viii.1946, *Blake* 16757 (culms tufted, creeping; flowering culms ascending or oblique up to 45 cm high; leaves green; spikelets paler).

Not previously recorded for the Northern Territory. Widely spread in the Tropics; in Australia previously known only from Queensland.

Eulalia mackinlayi (F. Muell.) S. T. Blake, comb. nov.

Pollinia mackinlayi F. Muell. ex Benth. Fl. Aust. 7: 527 (1878); Ewart & Davies, loc. cit. 26.

This species belongs in the genus *Eulalia* Kunth as now generally interpreted.

Sclerandrium grandiflorum S. T. Blake: sp. nov., affinis *S. intermedio* (A. Camus) C. E. Hubbard, a quo culmis glabris, racemis 2-4 (nec semper 2), spiculis sessilibus longioribus eorum lemmate superiore mutico vel breviter tantum aristulato differt

Culmi caespitosi, pro more 30-80 cm alti, erecti, graciles, teretes, simplices, 4-5-nodes, glabri laevesque. Foliorum vaginae firmae, ore longe laxeque barbatae, ceterum glabrae, striatae ceterum laeves, inferiores internodiis longiores, intermediae et superiores internodiis breviores; ligulae ciliolatae, subtruncatae, usque ad 1 mm longae; laminae basin versus attenuatae, apice gradatim acutae, usque ad 30 cm longae, usque ad 4 mm latae, firmae, supra scaberulae atque pilosae pilis prope ligulam usque ad 4 mm longis, marginibus quoque minute scaberulae, subtus

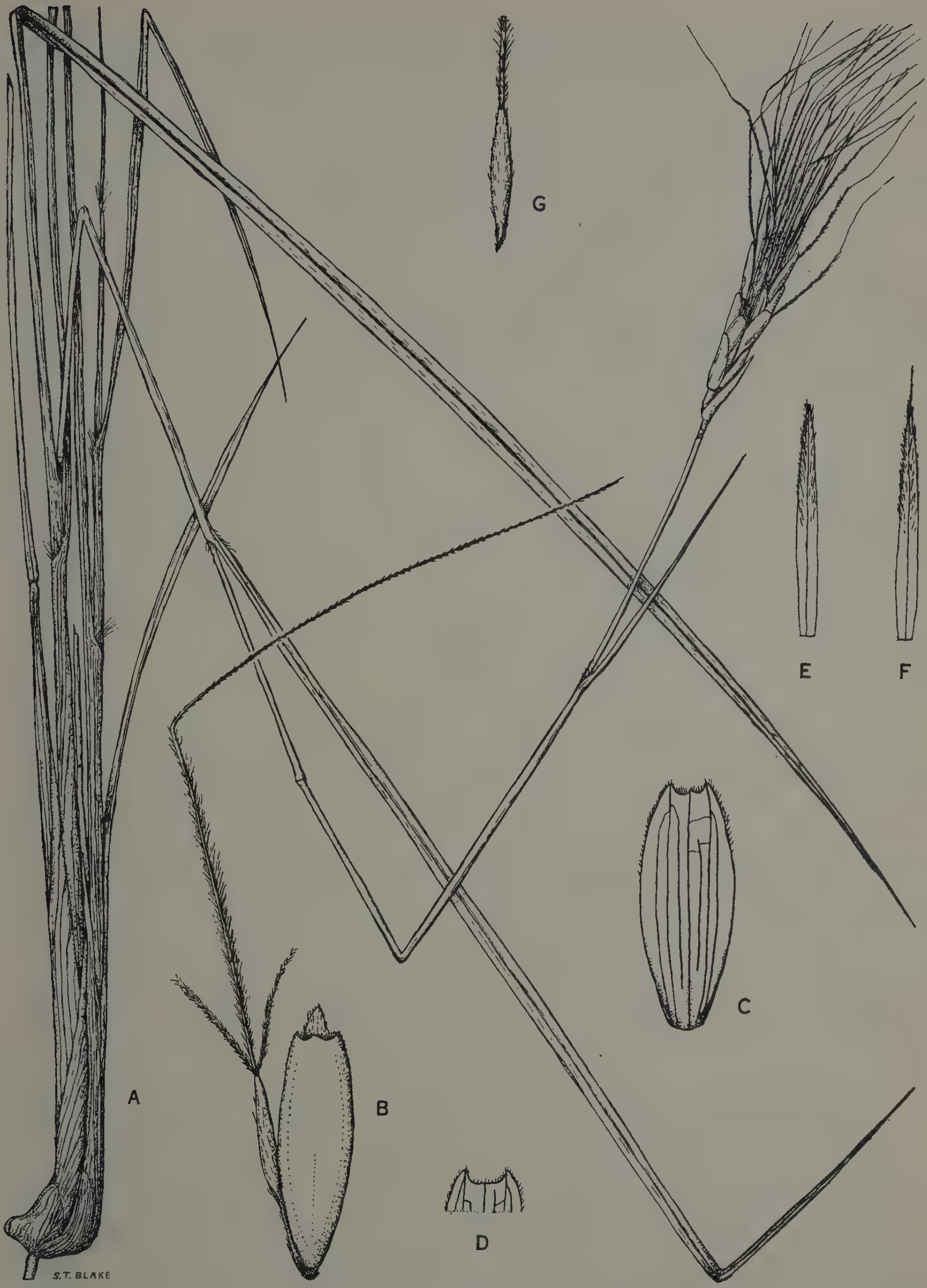


Fig. 1.—*Sclerandrium grandiflorum* S. T. Blake. *A*, portion of plant; *B*, a pair of spikelets; *C-F*, sessile spikelet — *C*, *D*, lower glume and tip of another, from within, *E*, *F*, lemma of upper floret; *G*, pedicelled spikelet. *A* × 1, *B-G* × 4. *F* from *Blake* 16539, remainder from type.

glabrae laevesque. Racemi 2-4, erecti, arcte appressi, 4-7 cm longi, robusti, plus minusve pedunculati pedunculis plus minusve connatis pilosis; axis primarius usque ad 5 mm longus, laxe pilosus; racemorum axis laxe pilosa, subtrigona vel compressa; pedicelli circa 2 mm longi, ciliati et latere abaxiali plus minusve pilosi. Spiculae sessiles 8.5-10 mm longae, anguste suboblongae, stramineae. Gluma inferior anguste elliptico-oblonga vel anguste obovato-oblonga, 2-3-dentata, marginibus superioribus apiceque breviter ciliata, dorso leviter convexo vel fere plano glabra laevisque, extus leviter intus distincte 7-nervis, infra apicem nervis anastomosantibus; gluma superior anguste ovata, obtusa, sursum marginibus ciliolata dorsoque plus minusve pilosa. Anthoecium inferum: lemma lanceolatum 7-8 mm longum, margines et apicem versus breviter pilosum; palea paullo brevior. Anthoecium superum: lemma circa 8 mm longum, acutissimum vel bidentatum, muticum vel (in paratypo) aristulatum aristula usque ad 2.5 mm longa, superne pilosum; palea anguste ovata, apicem versus breviter pilosa. Antherae circa 4 mm longae. Spiculae pedicellatae 5-5.5 (in paratypo usque ad 7) mm longae, fulvae. Gluma inferior (explanata) anguste ovato-oblonga, 5-nervis, pilis appressis albis demum fulvis induta; gluma superior glabrescens. Anthoecium inferum nullum. Anthoecium superum: lemma stipitiforme basi membranaceum 1-nerve, sed ab arista vix distinctum et cum ea 3-4 cm longum, in columna flexuosa pilosum; palea circa 3.5 mm longa, ciliolata.

Green, erect, tufted grass, usually 30-80 cm high. Culms erect, slender, terete, simple, 4-5-noded, glabrous, smooth. Leaves: sheaths loosely bearded at the mouth with long slender hairs, otherwise glabrous, striate, otherwise smooth, the lower ones longer than the internodes, the intermediate and upper ones shorter than the internodes; ligules ciliolate, subtruncate, up to 1 mm long; blades attenuate towards the base, gradually acute at the apex, up to 30 cm long, up to 4 mm wide, firm, scaberulous and silky-pilose on the upper surface with the hairs up to 4 mm long towards the ligule, minutely scabrous on the margins, glabrous and smooth on the lower surface. Racemes 2-4, erect, tightly appressed, 4-7 cm long, robust, more or less pedunculate with the peduncles more or less connate and pilose; primary axis short, up to 5 mm long, loosely hairy; axis of racemes loosely pilose, subtrigonous or compressed; pedicels about 2 mm long, ciliate and the abaxial face also more or less hairy. Sessile spikelets 8.5-10 mm long, narrowly suboblong, straw-coloured. Lower glume narrowly elliptic- or obovate-oblong, 2-3-toothed, shortly ciliate on the margins at and near the apex, glabrous and smooth on the slightly convex to nearly flat back, 7-nerved with the nerves inconspicuous on the back, but prominent within and anastomosing near the tip; upper glume narrowly ovate, obtuse, more or less hairy in the upper part on the back and margins. Lower floret: lemma lanceolate, 7-8 mm long, shortly hairy towards the tip and along the margins; palea slightly shorter. Upper floret: lemma about 8 mm long, very acute or bidentulate, muticous or with

a short awn up to 2.5 mm long, hairy in the upper part; palea narrowly ovate, shortly hairy towards the tip. Anthers about 4 mm long. Pedicelled spikelets 5-7 mm long, fulvous or brown. Lower glume narrowly ovate-oblong when flattened, 5-nerved, densely pilose with appressed white to fulvous hairs; upper glume glabrescent. Lower floret absent. Upper floret: lemma stipe-like, membranous, and 1-nerved near the base, scarcely distinct from the awn, and with this 3-4 cm long, pilose on the flexuose column; palea about 3.5 mm long, ciliolate.

NORTHERN TERRITORY.—Near Grove Hill, about 13° 28′ S., 131° 35′ E., in broad flat swampy drainage channel with sandy soil overlying clay, alt. about 90 m, 6.vi.1946, *Blake* 16360; near Hayes Creek, 13° 37′ S., 131° 26′ E., in swampy ground, alt. about 105 m, 10.vii.1946, *Blake* 16405 (TYPE); S. of mouth of Daly R., 13° 42′ S., 130° 15′ E., swampy ground near creek, 27 m, 21.vii.1946, *Blake* 16539 (PARATYPE). QUEENSLAND.—Cook district: Coen, swampy depressions with *Melaleuca* sp., about 195 m, 6.xii.1941, *Blake* 14542.

This second Australian species of *Sclerandrium* is rather conspicuously different from *S. truncatiglume* (F. Muell.) Stapf & Hubbard which is rather widely spread on shady stream banks and has glabrous leaves, more numerous (3-6), more slender, markedly brownish racemes with smaller spikelets with shorter awns, while the lower glume of the sessile spikelet is harder and markedly convex on the back. *S. grandiflorum* appears to be more closely allied to *S. intermedium* (A. Camus) C. E. Hubbard from Tong-king, known to me only from the original description and some remarks by C. E. Hubbard in his discussion on *S. truncatiglume* in Hook. Ic. Pl. *t.* 3262 (1935). The Asiatic plant is described as having hairy culms, 2 racemes with pale yellow hairs, and sessile spikelets 6-8 mm long with prominently awned upper lemmas.

Of the four collections cited, 16360 and 14542 consist of poor, over-mature material with most of the pedicelled spikelets fallen away. 16405 was selected as the type chiefly because of the abundance of material; the plants are rather smaller than the others and about at anthesis. Some details for the Latin description have been taken from 16539, which consists of 5 mature pieces with the racemes breaking up; this collection has to be regarded as a paratype (Fig. 1).

LAURACEAE

Cryptocarya cunninghamii Meissn. in DC. Prodr. 15 (1): 73 (1864)

C. glaucescens R. Br. var. *cunninghamii* (Meissn.) Benth. Fl. Aust. 5: 297 (1870).

WESTERN AUSTRALIA.—Kimberley Division: Hunter's River, Brunswick Bay, *A. Cunningham* (TYPE: 2 leaves seen). NORTHERN TERRITORY.—Darwin, in or near the Botanic Gardens, received Dec. 1939, *H. E. Hill*—*fl., fr.;* E. of Fog Bay, 12° 50′-51′ S., 130° 26′-27′ E., in patch of monsoon forest, shallow lateritic soil, 24 m, 12.viii.1946, *Blake* 16779 (tree, 7.5-12 m high; no buttresses; dense, rather broad dark green crown; grey bark with dense vertical irregular lines of fine lenticels; dark green leaves pallid green beneath; creamy white flowers; green fruit (? becoming black)—*fl.*, almost mature *fr., bark;* N. of Lake Finniss, 12° 19′ S., 131° 30′ E., monsoon forest, grey lateritic sand, 15.ix.1946, *Blake* 17016 (tree, 12 m high; grey, finely and shallowly fissured bark; dark green leaves subglaucous beneath; whitish flowers)—*fl.* QUEENSLAND.—Cook district: Flying Fish Point, April 1917, *Michael* 249 — *fr.*; Johnstone River, June 1916, *Michael* 140—*fl.*

The genus is new for the Northern Territory, for Cunningham's specimens cited by Ewart and Davies are from Western Australia. The species is also recorded here from Queensland for the first time. Bentham (loc. cit.) treated a number of more or less distinct forms as varieties of *C. glaucescens* R. Br. From *C. glaucescens* sens. str., *C. cunninghamii* differs in having leaves with much looser venation and scarcely glaucous beneath, and in the smaller, spherical fruits; from the other forms with more or less spherical fruits, it differs in the duller leaves with looser venation, the finer reticulations of which are not prominent, the subsessile flowers and fruits, and the fruit muticous because of the quite inconspicuous perianth. C. T. White noted that *Michael* 249 is a good match for the type and that Michael's other specimen has leaves rather more membranous.

LEGUMINOSAE-CAESALPINIOIDEAE

Peltophorum pterocarpum (DC.) Backer ex K. Heyne, Nutt. Pl. Ned.-Ind. ed. 2, 2: 755 (1927)

Inga pterocarpa DC. Prodr. 2: 441 (1825).

Caesalpinia inermis Roxb. Hort. Beng. 90 (1814), *nomen nudum;* Fl. Ind. 2: 367 (1832).

Poinciana roxburghii G. Don, Gen. Syst. 2: 433 (1832).

Caesalpinia ferruginea Decne. Nouv. Ann. Mus. Par. 3: 462 (1834).

Caesalpinia arborea Zoll. Nat. Geneesk. Archief 3: 65 (1846), fide Miq. Fl. Ind. Bat. 1: 112 (1855).

Peltophorum ferrugineum (Decne.) Benth. Fl. Aust. 2: 279 (1864); Ewart & Davies, loc. cit. 136.

Peltophorum inerme (Roxb.) Naves in Blanco, Fl. Filip. ed. 3, t. 335 (1877-83); F.-Vill. Nov. App. 69 (1880) *pro syn.;* Merr. Philip. J. Sci. 5 (C): 57 (1910).

Baryxylum inerme (Roxb.) Pierre, Fl. Forest. Cochinch. pl. 390 (1899).

Peltophorum roxburghii (G. Don) Degener, Fl. Hawaiiensis fam. 169 *b* (1938).

NORTHERN TERRITORY.—Near Beatrice Hill, about 12° 40′ S., 131° 18′ E., in monsoon forest, about 5 m, 11.ix.1946, *Blake* 16970 (tree about 10 m high; somewhat buttressed trunk; grey bark with rather coarse lenticels often in transverse rows; broad, dark green crown; dark green leaves paler beneath; rusty young shoots; reddish brown calyx with yellow margin; yellow petals with red-brown middle band)—*fl., fr.*

Widely spread through Malaysia to northern Australia and frequent in the "jungles" in the neighbourhood of Darwin; cultivated elsewhere. The species has usually been called *Peltophorum ferrugineum* (Decne.) Benth. or *P. inerme* (Roxb.) Naves, but from the synonymy given above *P. pterocarpum* (DC.) Backer is clearly the correct name. When Degener made the combination *P. roxburghii* (G. Don) Degener he overlooked the fact that *Caesalpinia inerme* Roxb. had been validly published in the same year as Don's name and since Roxburgh's epithet had already been transferred to *Peltophorum* his new combination was quite unnecessary.

Bauhinia cunninghamii (Benth.) Benth. Fl. Aust. 2: 295 (1864); Ewart & Davies, loc. cit. 132

Phanera cunninghamii Benth. in Miq. Pl. Jungh. 1: 264 (1852).
Bauhinia leichhardtii F. Muell. Trans. Phil. Inst. Vict. 3: 50 (1859).

NORTHERN TERRITORY.—Katherine, river levee, alt. 110 m, 23.vi.1946, *Blake* 16083 (tree, 7.5-10 m high; stout, more or less irregular trunk; open crown with obliquely ascending branches and drooping branchlets; dark grey hard fissured bark; dull green or subglaucous leaves; predominantly red flowers; rusty brown calyx; brownish pink petals; red stamens and pistil; curly pods; all material from one tree; local name: small-leaved bauhinia)—*fl., fr.*

A deciduous tree of the open forests of northern Australia; it sometimes forms nearly pure parkland on heavy soils (Plate 1, Fig. 3).

Piliostigma malabaricum (Roxb.) Benth. in Miq. Pl. Jungh. 261 (1852); Milne-Redhead, Hook. Ic. Pl. sub *t.* 3460 (1947)

Bauhinia malabarica Roxb. Fl. Ind. 2: 321 (1832); C. T. White, Proc. Roy. Soc. Qd. 47: 57 (1936).
Bauhinia acida Reinw. in Korth. Verhand. Nat. Gesch. Kruidk. 86 (1839-42).
Bauhinia castrata Haask. Flora 25 (2): beibl. 96 (1842).
Casparia castrata (Haask.) Haask. Pl. Jav. Rar. 412 (1848).
Piliostigma acidum (Reinw.) Benth. in Miq. Pl. Jungh. 261 (1852).
Bauhinia gilesii F. Muell. & F. M. Bail. Sth. Sci. Rec. 2: 151 (1882); Ewart & Davies, loc. cit. 132.
Bauhinia hawkesiana F. M. Bail. Qd. Agric. J. 15: 897 (1905).

NORTHERN TERRITORY.—Bank of Daly R., 13° 52′ S., 131° 4′ E., in fringing forest, about 30 m, 16.vii.1946, *Blake* 16476 (tree of 9 m; grey, rough, furrowed bark; broad crown of dull green leaves paler beneath)—*fr.*

Occasional in fringing forest, more rarely on heavy soil behind levees. Widely spread from India to northern Queensland. The type of *B. gilesii* came from Springvale Station, Katherine, but Ewart and Davies merely stated "*B. Gilesii,* F.v.M. and Bail.; recorded in National Herbarium Census from North Australia."

As White pointed out, the type material of *Bauhinia gilesii* and *B. hawkesiana* is not distinguishable from *B. malabarica.* Milne-Redhead (loc. cit.) took up Hochstetter's name *Piliostigma* for a group of three species of deciduous trees from Africa, Asia, and Australia, with dioecious flowers, turbinate calyx-tube with a 4-5-fid limb, cushion-like stigma on a very short style, and an indehiscent pod with seeds immersed in pulp in two or more series. I have examined the types of *B. gilesii* and *B. hawkesiana* and Malaysian specimens of *B. malabarica;* the rest of the synonymy has been taken from Milne-Redhead's paper.

The species was called *Bauhinia malabarica* in the account of the vegetation of the Katherine-Darwin Region in C.S.I.R.O. Aust. Land Res. Ser. No. 1 (1953).

Cassia sophera L. Sp. Pl. 379 (1753); Ewart & Davies, loc. cit. 135

NORTHERN TERRITORY.—Lake Nash, weed near buildings, 189 m, 29.v.1947, *Blake* 17960 (bushy annual 60-120 cm high; dull subglaucous leaves paler beneath; yellow flowers)—*fl., fr.*

A cosmotropical weed of American origin; this is only the second record for the Northern Territory.

Cassia venusta F. Muell. Fragm. 1: 165 (1859); Benth. op. cit. 2: 284 (1864); Ewart & Davies, loc. cit. 135

NORTHERN TERRITORY.—O.T. Station, 16° 37′ S., 135° 3′ E., rough quartzite country, among *Triodia pungens*, alt. 180 m, 8.v.1947, *Blake* 17661 (erect, more or less glaucous shrub 1-1.2 m high with yellowish branches; flowers yellow)—*fl.*, *fr.*

Widely spread in northern Australia, chiefly in dry, barren country.

Cassia notabilis F. Muell. Fragm. 3: 28 (1862); Benth. op. cit. 2: 284 (1864); Ewart & Davies, loc. cit. 135

NORTHERN TERRITORY.—Tennant Creek, with *Triodia* in mixed open low scrub on flat ground about 240 m, 17.vi.1946, *Blake* 16006 (hoary, soft-wooded, bushy shrub of 1.2 m; twigs and rhachis yellowish; leaves hoary; flowers yellow)—*fl.*, very young *fr.*

A distinctive but very poorly known species not certainly known from outside the Northern Territory.

Cassia pruinosa F. Muell. Fragm. 3: 48 (1862); Benth. op. cit. 2: 286 (1864); Ewart & Davies, loc. cit. 135

QUEENSLAND.—Burke district: On Barkly Downs Station, 20° 22′ S., 138° 25′ E., in open scrub of chiefly *Acacia* and *Triodia* on red stony soil, 238 m, 27.v.1947, *Blake* 17941 (silvery-looking sparse shrub of 1.2-1.5 m with yellow flowers)—*fl.*

Widely spread in the drier parts of Australia.

Cassia mimosoides L. Sp. Pl. 379 (1753); Benth. op. cit. 2: 291 (1864); Ewart & Davies, loc. cit. 135

NORTHERN TERRITORY.—Near Hayes Creek, 13° 35½′ S., 131° 28′ E., on damp sandy soil carrying *Banksia, Acacia, Verticordia, Pandanus*, etc., alt. about 107 m, 27.vi.1946, *Blake* 16215 (erect branched annual (?) about 90 cm high with dull, subglaucous leaves and yellow flowers)—*fl.*, *fr.*

Widely distributed through the northern and eastern parts of Australia, extending through Malaysia to southern China and India.

Petalostylis labicheoides R. Br. App. Sturt Exped. 80 (1849); Benth. op. cit. 2: 292 (1864); Ewart & Davies, loc. cit. 132

NORTHERN TERRITORY.—On Rockhampton Downs Station, 19° 2′ S., 135° 9′ E., in *Acacia-Triodia* scrub on red lateritic soil, 227 m, 19.v.1947, *Blake* 17867 (green bush to 2 m; yellow flowers)—*fl.*

Very common along roadsides through the desert scrub N. and E. of Tennant Creek; also widely spread in the drier parts of Western Australia, Queensland, New South Wales, and South Australia.

Bentham (loc. cit.) spelt the generic name *Petalostyles* and cited page 17 as the place of publication.

LEGUMINOSAE-MIMOSOIDEAE

Mimosa acanthocarpa Poir. Encycl. Suppl. 5: 529 (1817)

NORTHERN TERRITORY.—Darwin, Botanic Gardens, August 1946, *Christian*—*fr.*

Not previously recorded for Australia; a native of Mexico, now naturalized as a bad weed at Darwin.

Albizia canescens Benth. Fl. Aust. 2: 423 (1864)

NORTHERN TERRITORY.—Near Kathleen Falls, Flora R., very occasional in very open *Eucalyptus papuana* — *Tristania* forest, crumbly dark grey soil, about 110 m, 16.x.1946, *Blake* 17238 (deciduous tree, about 9 m high; yellowish grey rough bark; rather spreading branches; green leaves)—*fr.*

Previously known only from Queensland and (?) Western Australia, and only once observed in the Northern Territory in 1946. This is also the first record of the genus from the Northern Territory, for Henne's specimens of *A. procera* (Roxb.) Benth. cited by Ewart and Davies (loc. cit. 122) came from eastern Queensland (Gloucester I.).

The generic name has usually been spelled *Albizzia,* but according to Sweet (Amer. Midl. Nat. 30: 510 (1945) quoted by G. H. M. Lawrence, Gent. Herb. 8: 44 (1949)), Durazzini consistently used one "z" in the original paper (Mag. Toscan. 3 (4): 10, 11, 13 and plate (1772)).

Pithecellobium moniliforme (DC.) Benth. Lond. J. Bot. 3: 211 (1844) and Fl. Aust. 2: 424 (1864); Ewart & Davies, loc. cit. 122 (all as *Pithecolobium moniliferum*)

Inga moniliformis DC. Prodr. 2: 440 (1825).

Albizzia monilifera (DC.) F. Muell. J. Bot. 10: 10 (1872) and Icon. Aust. Sp. Acacia *t.* 123 (1888).

NORTHERN TERRITORY.—Near Beatrice Hill, about 12° 40′ S., 131° 18′ E., in monsoon forest near lagoons, about 5 m, 11.ix.1946, *Blake* 16969 (small crooked tree, usually in clumps, up to 7.5 m high; grey, scaly bark; green leaves, paler beneath; nearly white flowers; flowering and fruiting specimens all from same tree)—*fl., fr.;* same locality and date, in monsoon forest near lagoons and streams, *Blake* 16969*A* (dense, many-stemmed shrub of 3 m; pale grey finely fissured bark; dark shining green leaves, paler beneath; nearly white flowers)—*fl.*

Northern parts of the Northern Territory and Queensland, chiefly in fringing forests and there locally abundant.

The generic name has been variously spelt *Pithecellobium, Pithecollobium,* and *Pithecolobium;* with the first-mentioned spelling, it is conserved against *Zygia* Boehm. Bentham (loc. cit.), in transferring the species from *Inga,* misspelt the epithet "*moniliferum*" and this spelling has been adopted by later authors including those of *Index Kewensis;* it is so evidently a slip of the pen (Bentham cited *Inga monilifera* DC.) that the combination as cited above should be attributed to Bentham (Art. 82 of the International Code of Botanical Nomenclature). The species was originally described from Timor.

Erythrophleum chlorostachys (F. Muell.) Baill. Hist. Pl. 2: 150 (1870)

Laboucheria chlorostachys F. Muell. J. Linn. Soc. (Bot.) 3: 159 (1859).

Erythrophloeum laboucherii F. Muell. ex Benth. Fl. Aust. 2: 297 (1864); Ewart & Davies, loc. cit. 132.

NORTHERN TERRITORY.—Berry Springs, near Middle Arm, Port Darwin, in *Eucalyptus miniata*—*E. tetrodonta*-dominant open mixed forest, stony sandy soil, about 15 m, 7.ix.1946, *Blake* 16948 (tree to 12 m high; dark grey, coarsely tessellated, hard bark; green leaves; whitish flowers)—*fl., fr.;* Katherine, river levee, mixed open forest, reddish sandy soil, 107 m, 8.x.1946, *Blake* 17186 (tree, 10 m high; grey, coarsely scaly bark; often broad crown; green, more or less deciduous leaves; creamy flowers)—*fl. fr.*

A more or less deciduous tree widely spread in the open forests of northern Australia and universally known as "ironwood". The leaves contain a very deadly alkaloid. It yields an excellent timber, quite resistant to termites.

The generic name has commonly been spelt *Erythrophloeum* and the authorship quoted as "Afzelius ex R. Brown in Tuckey, Congo, 430 (1818)" (cf. *Index Kewensis* 897 (1893)). On the page cited there is merely the remark that "One of these is Erythrophleum of Afzelius, the Red Water Tree of Sierra Leone . . . . ." This does not constitute valid publication of the name as there is no description nor a reference to a previously published description. Later, in Narrative of Travels and Discoveries in Northern and Coastal Africa *by* . . . . Denham and . . . . Clapperton, Appendix 234 (1826), Brown made a few remarks that might be regarded as a description. This passage reads: "*Erythrophleum* . . . . more probably belongs to Mimoseae, although its stamina are perigynous. In this genus both calyx and corolla are perfectly regular and their aestivation, if not strictly valvular, is at least not manifestly imbricate, though the flower buds are neither acute nor angular."*

G. Don, Syst. Pl. 2: 423-4 (1832), gave a good description of the genus and of *E. guineense*. Don cited "E. guineense (G. Don, in Edinb. phil. journ. 1824)" but in this publication the generic name occurs in a list without any description.

Brown and Don consistently spelt the name *Erythrophleum*. Reichenbach (Consp. 157 (1828)) altered the spelling to *Erythrophlaeum,* and this form was adopted by Endlicher, Gen. Pl. 1323 (1840), by F. Mueller in J. Roy. Soc. N.S.W. **15**: 205 (1882), First Census 43 (1882), and Second Census 74 (1889), and by Ewart and Davies, loc. cit. Bentham (loc. cit.) spelt the name *Erythrophloeum* and this form has been the one commonly used in Australia and elsewhere and it may be desirable to conserve it.

Dichrostachys spicata (F. Muell.) Domin, Bibl. Bot. **89**: 247 (1926)

Neptunia spicata F. Muell. Fragm. **3**: 151 (1863).

Dichrostachys muelleri Benth. Fl. Aust. **2**: 299 (1864); Ewart & Davies, loc. cit. 132.

NORTHERN TERRITORY.—NE. of Anthony Lagoon, 17° 49′ S., 135° 38′ E., on low rise sparsely timbered with small trees, yellowish stony soil, 227 m, 15.v.1947, *Blake*

---

* Brown's remarks are quoted from "The Miscellaneous Botanical Works of Robert Brown 1: 111, 290 (Ray Society: London, 1866).

17797 (bushy-headed shrubby tree to 3 m; grey, compact, irregularly fissured bark; dull, subglaucous leaves; upper part of inflorescence yellow, lower part pink or white) —*fl.*, *fr.*

This is the second record of this plant from the Northern Territory; it was recorded from Western Australia by Domin (loc. cit.).

Neptunia monosperma F. Muell. ex Benth. Fl. Aust. 2: 300 (1864); Ewart & Davies, loc. cit. 131

NORTHERN TERRITORY.—O.T. Station, 16° 37′ S., 135° 3′ E., in *Dichanthium-Eulalia* grassland, heavy yellow-grey melonholey soil, 177 m, 10.v.1947, *Blake* 17709 (perennial with very oblique or spreading stems up to 60 cm long; dull light green leaves)—*fr.*

Northern Territory and Queensland.

Neptunia gracilis Benth. Lond. J. Bot. 4: 355 (1842), Fl. Aust. 2: 300 (1864); Ewart & Davies, loc. cit. 131

NORTHERN TERRITORY.—O.T. Station, 16° 37′ S., 135° 3′ E., in *Dichanthium-Eulalia* grassland heavy yellow-grey melonholey soil, 177 m, chiefly at edge of melonholes, 9.v.1947, *Blake* 17697 (woody base; more or less trailing stems up to 60 cm long; dull green leaves, subglaucous beneath; pale yellow flowers)—*fl.*, *fr.*

This is the first definite record of this species from the Northern Territory; it is widely spread in Queensland.

LEGUMINOSAE-PAPILIONATAE

Dendrolobium stipatum S. T. Blake; sp. nov., affinis *D. umbellato* (L.) Benth. sed habitu suffrutescenti, pedunculo brevissimo vel nullo, pedicellis longioribus, bracteis bracteolisque subulatis differt

Suffrutex 30-60 cm altus, pilis appressis fere rectis fere ubique pubescens et in novellis subsericeus. Caules plures e basi lignosa orientes, plus minusve erecti, graciles, simplices vel ramosi. Stipulae ex basi plus minusve deltoidea subulato-acuminatae, striatae, extra appresse pubescentes intus glabrae, basi breviter connatae. Folia pinnatim trifoliata; petioli 7-12 mm longi; petiolulus terminalis 5-13 mm longus, laterali 1.5-2.5 mm longi; stipellae subulatae, 1.4-2 mm longae. Foliola elliptica vel admodum ovata, obtusa vel emarginata, basi rotundata vel cuneata, supra viridia subtus multo pallidiora, utrinque parcius appresso-pubescentia, nervis utrinsecus costam 6-10 cum costa reticulationibusque utrinque prominulis praedita; foliolum terminale 4-6.5 cm longum, 1.5-3.3 cm latum (duplo usque $2\frac{1}{2}$-plo longiora quam lata); foliola lateralia paullo minora, interdum angustiora. Inflorescentiae axillares, pluriflorae, ob racemos brevissimos umbelliformes, sessiles vel fere sessiles (pedunculis ut plurimum 1 mm longis); pedicelli filiformes, pro more 7-15 mm longi. Bracteae sub pedicellis subulatae, 1.7-2.5 mm longae; bracteolae 2 apice pedicelli sitae, subulatae, circa 1.5 mm longae. Calyx 5.5-6 mm longus, appresse pilosus, circum ad medium fissus; tubus subturbinatus; lobi subovato-triangulares, subacuminati, 2 superiores fere vel usque ad apicem connati, tubo paulisper breviores, inferior lateralesque paullo angustiores, tubum subaequantes. Corolla glabra: vexillum suborbiculare in unguem contractum, supra ungui callosum, circa 11 mm longum (ungue inclusa) et 9 mm latum; alae carina admodum longiores et eam leviter adhaerentes, unguiculatae atque calcaratae, circa 12 mm longae; carina recta, apice obtuse rotundata, circa 11 mm longa. Stamina monadelpha, alte (usque ad quattuor partes longitudinis) connata. Ovarium sessile, dense hirsutum. Legumen sessile, indehiscens, pro more 3-4-articulatum, plus minusve incurvum, margine supero incrassato vix constrictum, margine infero leviter constrictum, appresse pubescens (nec scabrum nec uncinato-hispidum); isthmi dimidio latitudine leguminis paullo angustiores; articuli oblongo-subreniformes, 6-8 mm longi, 4.5-5 mm lati, leviter reticulati. Hilum seminis ovale marginibus haud incrassatum.

Subshrub, 30-60 cm high, pubescent almost throughout with appressed, nearly straight hairs, the young shoots rather silky. Stems several from a woody base, more or less erect, slender, simple or branched. Stipules subulate-acuminate from a more or less deltoid base, striate, appressedly hairy outside, glabrous within, shortly connate at the base. Leaves pinnately trifoliate; petioles 7-12 mm long; terminal petiolule 5-13 mm long, lateral ones 1.5-2.5 mm long; stipellae subulate, 1.4-2 mm long. Leaflets elliptic or somewhat ovate, obtuse or emarginate, rounded or cuneate at the base, green above, much paler beneath, both sides sparsely appressed-pubescent, the lateral nerves 6-10 on each side of the midrib and with it and the reticulations prominent on both surfaces; terminal leaflet 4-6.5 cm long, 1.5-3.3 cm wide (2-2.5 times as long as wide), the lateral ones slightly smaller and sometimes rather narrower. Inflorescences axillary, umbel-like because of the extreme shortening of the raceme, several-flowered, sessile or subsessile with the peduncle not exceeding 1 mm in length; pedicels filiform, mostly 7-15 mm long, each with a subulate bract 1.7-2.5 mm long at the base and 2 subulate, more or less persistent bracteoles at the top about 1.5 mm long. Calyx 5.5-6 mm long, appressedly hairy, divided to about the middle; tube subturbinate; lobes subovate-triangular, subacuminate, the 2 upper ones connate almost or quite to the top, slightly shorter than the tube; lower lobe slightly narrower than the lateral ones, about as long as the tube. Corolla glabrous; standard suborbicular, contracted into a distinct claw above which is a distinct callosity, about 11 mm long (including the claw) and 9 mm wide; wings slightly longer than the keel and lightly adhering to it, clawed and spurred, about 12 mm long; keel straight, obtusely rounded at the apex, about 11 mm long. Stamens monadelphous, connate as far as 4/5 their length. Ovary sessile, densely hirsute. Pod sessile, indehiscent, more or less incurved, appressedly pubescent (neither scabrous nor uncinate-hispid), the upper margin thickened but scarcely constricted between the seeds, the lower margin slightly constricted so that the isthmus is about ½ as wide as the pod; articles mostly 3 or 4, oblong-subreniform, 6-8 mm long, 4.5-5 mm wide, slightly reticulate; hilum of seed oval, not thickened at the margins.

NORTHERN TERRITORY.—E. of mouth of Daly R., 13° 23′ S., 130° 32′ E., open *Pandanus-Eucalyptus* forest, grey sandy soil, 44 m, 30.vii.1946, *Blake* 16670 (undershrub with tufted, erect stems 30-60 cm high; sage-green leaves subglaucous beneath; petals pink, the standard whitish in upper part)—*fl.*, *fr.* (TYPE).

Though closely similar in many respects to *Dendrolobium umbellatum* (L.) Benth., this new species appears to differ sharply from this and other species known to me in the sessile or subsessile inflorescence with long pedicels, while the subulate bracts and bracteoles, and the coriaceous, regularly rounded or emarginate leaflets are also noteworthy (Plate 2). Except that there are 2-4 ovules instead of 1-2, the specimens agree with the description of *Holtzea umbellata* Schindl. Repert. Nov. Spec. Regn. Veg. **22**: 285 (1926). Schindler has not indicated how his *Holtzea* (which is monotypic) differs from other genera, and from the description I can find nothing but the few ovules to distinguish it from *Dendrolobium* discussed by him, op. cit. **20**: 278-9 (1924).

Desmodium polyneurum S. T. Blake; sp. nov., in subgenus *Dollineram* (Endl.) Schindl. prope *D. karensium* Kurz inserenda, a qua specie pilis indumenti mollibus rectiusculis vix uncinatis atque leguminis articulis paucis differt.

Suffrutex 60-90 cm altus, petalis staminibusque exceptis pilis brevibus rectiusculis canescentibus vel fulvescentibus ubique indutus. Caules plures erecti, plus minusve striolati, sursum angulati, pilis crispulis ascendentibus vel recurvis partim capitatis molliter pubescentes. Stipulae facillime deciduae, subdeltoideae sed fere ad medium connatae, omnino pubescentes, 3-5.5 mm longae. Folia semper pinnatim trifoliata; petioli pubescentes, 5-20 mm longi; stipellae setaceae 1.5-2 mm longae; petiolulus terminalis 10-23 mm longus, laterali 2-2.5 mm longi. Foliola dense et breviter et appresse sericeo-pubescentia, nervis lateralibus validis 10-13 utrinsecus costam validam praedita, inter eos leviter reticulata; foliolum terminale obovatum, apice late rotundatum vel plus minusve emarginatum interdum apiculatum, basi anguste rotundatum vel plus minusve cuneatum, pro more 4 cm longum et 2.3 cm latum usque ad 7.5 cm longum et 4.5 cm latum; folia lateralia paullo minora, plus oblonga, pro more 3.5 cm longa et 1.7 cm lata usque ad 7 cm longa et 3.4 cm lata. Flores vel singuli vel bini vel terni in racemos pedunculatos axillares foliis conspicue longiores dispositi; pedunculi validi compressi usque ad 7 cm longi; pedicelli 2-7 mm longi; bracteae ovatae, acuminatae, 2-3 mm longae, extus appresse hirsutae intus striatae, sub anthesi caducae; bracteolae basi calycis insertae, bracteis similes. Calyx circa 7.5 mm longus, pubescens; tubus 3 mm longus, basi obtusus, sursum gradatim ampliatus; lobi lanceolati, acuti, 2 superiores primum fere ad apicem connati et labium superum latum subacutum efformantes, tandem separantes. Vexillum obovatum, basi cuneatum plus minusve unguiculatum, 10 mm longum, 7 mm latum. Alae cum carina

aequilonga adhaerentes, 10 mm longae, basin versus calcaratae, unguiculatae. Carina leviter incurva, obtusiuscula. Stamen vexillare cum ceteris inferne connatum. Ovarium hirsutum; stylus basin versus laxe pilosus. Legumen inter semina marginibus ambobus constrictum, dense pubescens; articuli pro more 2 vel 3, raro 1 vel 4, longitudinaliter ovales, subsymmetrici, circiter 7 mm longi et 5 mm lati, ? indehiscentes; semina matura haud visa; hilum suborbiculare marginibus incrassatum.

Subshrub, 60-90 cm high, except for the petals and stamens completely covered with short, nearly straight, hoary or yellowish hairs. Stems numerous from a woody stock, erect, more or less striate, angular in the upper part, softly pubescent with ascending or recurved crisped hairs, some of which are capitate. Stipules nearly deltoid, connate nearly to the middle, pubescent throughout, 3-5.5 mm long, readily deciduous. Leaves all pinnately trifoliate; petioles pubescent, 5-20 mm long; stipellae setaceous, 1.5-2 mm long; terminal petiolule 10-23 mm long, the lateral ones 2-2.5 mm long. Leaflets densely, shortly, and appressedly silky-pubescent, with 10-13 prominent veins on each side of the stout midrib and lightly reticulate between; terminal leaflet obovate, broadly rounded or emarginate at the top and sometimes apiculate, narrowly rounded or more or less cuneate at the base, between 1.6 times and twice as long as wide, 4-7.5 cm long and 2.3-4.5 cm wide; lateral leaflets slightly smaller, more oblong, usually 3.5-7 cm long and 1.7-3.4 cm wide. Flowers solitary or binate or ternate in pedunculate axillary racemes much longer than the leaves; peduncles stout, compressed, up to 7 cm long; pedicels 2-7 mm long; bracts ovate, acuminate, 2-3 mm long, appressed-hirsute on the outside, striate within, falling as the flower expands; bracteoles 2 at the base of the calyx, similar to the bracts. Calyx about 7.5 mm long, pubescent; tube 3 mm long, obtuse at the base, gradually widened upwards; lobes lanceolate, acute, the 2 upper ones at first connate nearly to the tip and forming a broad, subacute upper lip, finally separating. Corolla: standard obovate, cuneate, and more or less clawed at the base, about 10 mm long and 7 mm wide; wings adhering to the keel, 10 mm long, clawed, spurred near the base; keel as long as the wings, subobtuse, slightly incurved. Stamens monadelphous. Ovary hirsute; lower part of style with spreading hairs. Pod densely pubescent, both margins constricted between the seeds; articles usually 2 or 3, rarely 1 or 4, longitudinally oval and nearly symmetrical, about 7 mm long and 5 mm wide, indehiscent (?); seeds with suborbicular hilum with thickened margin, not seen mature.

NORTHERN TERRITORY.—Near Station Creek, 13° 42½′ S., 131° 4′ E., gentle slope in open forest, about 53 m, 15.vii.1946, *Blake* 16474 (perennial with tufted, oblique to erect stems 60-90 cm high; slightly olive-green leaves paler beneath; white flowers)—*fl., fr.* (TYPE); Near Daly R., 13° 55′ S., 131° 12′ E., common on river frontages, about 46 m, 1.vii.1946, *Blake* 16278 (woody base; stems tufted, oblique, mostly 60-90 cm high; subglaucous leaves paler beneath; whitish flowers)—*fl.*

A rather distinctive species because of the close, even, soft indumentum, neat leaflets with rather numerous lateral veins, racemes

in the axils of many of the leaves, early deciduous stipules, well-developed though small bracteoles, and few but large articles of the pod (Plate 3). I have been unable to reconcile the species with any of the generally accepted related genera or with any of the groups within *Desmodium* sens. lat. that have been treated by Schindler as distinct genera. Particularly because the seed has a swollen ring-like margin to the hilum, the species is to be placed in subgen. *Dollinera* (Endl.) Schindl. op. cit. 22: 262, and the 2 bracteoles close under the calyx would suggest its arrangement in sect. *Tiliifolia* Schindl. loc. cit. 263. The nearly symmetrical pod-articles would bring *D. polyneurum* near *D. karensium* Kurz, *D. prainii* Schindl., and *D. sequax* Wall. The last-mentioned, of which I have seen several specimens from India and Malaysia, is readily distinguished by its sinuate-margined leaflets with fewer lateral veins, the looser and harsher indumentum, the smaller flowers, and the smaller, more numerous, more harshly hairy pod-articles. The 2 other species are known to me only from descriptions and the notes published by Schindler in his key and op. cit. **21**: 1-2. Both appear to have more numerous articles, those of *D. prainii* being smaller, scarcely longer than wide, nearly glabrous, and distinctly reticulate. *D. karensium* appears also to have acuminate leaflets and a much harsher indumentum.

MELIACEAE

Xylocarpus australasicus Ridl. Kew Bull. **1938**: 291 (1938)

NORTHERN TERRITORY.—About 12° 40′ S., 131° 25′ E., muddy bank of small creek at its junction with Adelaide R., 14.ix.1946, *Blake* 16996 (narrow-crowned tree to 9 m high; cylindrical trunk with grey, long-flaky bark; stout, narrowly conical pneumatophores; rather light green leaves; creamy white flowers)—*fl.*

Specimens of this mangrove were referred to *Carapa moluccensis* Lam. by Bentham (op. cit. **1**: 387 (1863)) and Ewart and Davies (loc. cit. 159). Most modern authors treat *Xylocarpus* as generically distinct from *Carapa* Aubl. because of the woody, not corky, pericarp, fewer leaflets, and smaller inflorescences with smaller flowers. *Carapa* is confined to tropical eastern South America and tropical western Africa, while *Xylocarpus* ranges from tropical eastern Africa through India, Malaysia, northern Australia, to Polynesia. *Xylocarpus australasicus* resembles *X. moluccensis* (Lam.) M. Roem. in having flaky bark and peg-like pneumatophores, but differs in having smaller and more obtuse leaflets, smaller panicles and flowers, and a slightly dilated base to the staminal tube. It has only been recorded from Queensland and the Northern Territory, but it appears also to be in Papua.

Owenia vernicosa F. Muell. Fragm. **3**: 15 (1862); Benth. op. cit. **1**: 385 (1863); Ewart and Davies, loc. cit., 159

NORTHERN TERRITORY.—Katherine, river levee, mixed open forest, 110 m, 19.x.1946, *Blake* 17263 (tree to 12 m high with deciduous leaves; few, suberect branches; grey, rather coarsely scaly bark; rather light green leaves clustered at end of twigs; greenish white flowers)—*fl.*

Northern Australia, in *Eucalyptus* forest; leafless in the dry season and flowering with the new leaves.

Vavaea australiana S. T. Blake; sp. nov. affinis *V. chalmersii* C. DC., *V. archboldianae* Merr. & Perry, et *V. ledermannii* Harms (speciebus novoguineensibus), sed foliorum nervis lateralibus minus divergentibus, tubo stamineo profundius (ultra medium) inciso et ejus laciniis pro majore parte utrinque villosis, atque antheris dorso longe pilosis ab omnibus conspicue differt

Arbor 6 m alta, floribus exceptis fere omnino glabra, cortice griseo lenticellato praedita. Ramuli apice primo puberuli, mox glabrescentes. Folia aggregata, alterna, conspicue petiolata; petioli 1.0-2.0 cm longi, basim versus tenuiter puberuli vel glabrescentes; laminae glaberrimae, chartaceae, anguste obovatae vel late oblanceolatae, obtuse et plerumque breviter acuminatae (acumine circiter 0.5-2 cm longo), basim versus longe cuneatae, margine integrae vel leviter undulatae, 10-23 cm longae, 4-9 cm latae, longitudine duplam latitudinem usque ad duplam et tres quintas partes aequante, nervis lateralibus fere rectis vel (praecipue superioribus) leviter curvis 7-9 untrinsecus costam orientibus et cum ea angulum circa 40° facientibus. Inflorescentiae corymbosae, pro more 9-21-florae, floribus ipsis exceptis glabrae, longe pedunculatae sed foliis breviores; pedunculi compressi, 5-10 cm longi; rami primarii 3-7, usque ad 2.5 cm longi; pedicelli 1.4-1.6 mm longi. Flores albi tandem flavescentes. Calyx breviter tenuiterque pubescens, 1.6-1.8 mm longus, leviter 5-6-lobus, lobis oblato-triangularibus acutis, 0.7-0.9 mm longis, 1.0-1.2 mm latis. Petala 5-6, late linearia, obtusa, circa 5-6 mm longa, circa 1.2 mm lata, prope basim interiorem glabra, alibi breviter denseque pubescens. Tubus stamineus (antheris inclusis) circiter 3 mm longus, ad circiter duas partes altitudinis in 15-18 lacinias fissus; pars integra glabra; laciniae basim versus utrinque glabrae, sursum utrinque dense villosae, 5-6 aliis paullo breviores; antherae dorso pilosae, minute apiculatae, circa 0.7 mm longae. Discus ad tubo stamineo adnatus, circa 0.7 mm latus, facie interiore sursum appresse hirsutus. Ovarium hirsutum, 2-loculare; stylus circa 2 mm longus, prope apicem glaber, in majore parte appresse hirsutus; stigma capitatum.

Tree 6 m high with grey lenticellate bark, the very young shoots silky. Twigs puberulous at the tips when young soon becoming glabrous. Leaves prominently petiolate; petioles 1.0-2.0 cm long, finely puberulous towards the base or glabrescent; blades quite glabrous, chartaceous, narrowly obovate or broadly oblanceolate (2-2.6 times as long as wide), obtusely and usually shortly acuminate (acumen about 0.5-2 cm long), long-cuneate at the base, entire or somewhat undulate at the margins, 10-23 cm long, 4-9 cm wide, with 7-9 pairs of lateral veins which are nearly straight or (particularly the upper ones) gently curved throughout, at an angle of about 40° with the midrib. Inflorescence corymbose, mostly 9-21-flowered, glabrous except the flowers, long-pedunculate but shorter than the leaves;

peduncles compressed, 5-10 cm long; primary branches 3-7, up to 2.5 cm long; pedicels 1.4-1.6 mm long. Flowers white turning yellow. Calyx shortly and faintly pubescent, 1.6-1.8 mm long, shallowly 5-6-lobed, the lobes triangular, broader than long, acute, 0.7-0.9 mm long and 1.0-1.2 mm wide. Petals 5-6, broadly linear, obtuse, about 5-6 mm long, about 1.2 mm wide, glabrous inside near the base, elsewhere shortly and closely pubescent. Staminal tube about 3 mm long including the anthers, cleft for about 2/3 its height into 15-18 lobes, entire part glabrous; lobes glabrous on both sides near the base, densely woolly on both sides elsewhere, 5 or 6 of them slightly shorter than the others; anthers pilose on the back, minutely apiculate, about 0.7 mm long. Disk united to the staminal tube, appressed-hirsute on the upper part of the inner face, about 0.7 mm high. Ovary hirsute, 2-celled; style appressed-hirsute to near the glabrous apex, about 2 mm long; stigma capitate.

NORTHERN TERRITORY.—Sandstone tableland between Gerowie Creek and Mary R., 13° 30′ S., 132° E., in fringing forest on banks of small perennial stream, alt. about 305 m, 4.x.1946, *Blake* 17168 (TYPE) (tree, 6 m high; grey, lenticellate bark; green leaves paler beneath; white flowers turning yellow)—*fl.*

This genus has not previously been recorded from Australia except for the bare mention by Merrill, *Plant Life of the Pacific World*, p. 213 (1945), and Blake, Aust. J. Bot. **1**: 331 (1953) (as *Vavea*). About 20 other species are known from Malaysia, Melanesia, and Polynesia, ranging from the Philippine Is. and New Guinea to Fiji and Tonga. It shares with *Turraea*, *Nurmonia*, and some species of *Munronia* the unusual feature (for the Meliaceae) of simple leaves, but it differs from these in the absence of endosperm in the seeds, the staminal tube with anthers terminating each of the numerous hairy lobes and a disk adnate to its base, the hairy ovary with only 2-4 cells, and from at least most species in the structure of the inflorescence, and habit.

The outstanding characters of *V. australiana* are the prominently petiolate, glabrous leaves with rather few and mostly nearly straight veins at a rather acute angle with the midrib, the shallowly lobed calyx, the deeply cleft staminal tube with the lobes villous on both sides nearly throughout, the long hairs on the backs of the anthers, and the 2-celled ovary (Plate 4). It appears to be most closely allied to some of the New Guinea species, particularly *V. chalmersii* C. DC., *V. archboldiana* Merr. & Perry, and *V. ledermannii* Harms, with which it shares the characters of nearly complete absence of indumentum, leaves with prominent petioles and relatively few lateral veins, rather small flowers, small calyx-teeth, and 2-celled ovary. It differs from all of these in the rather acute angle made by the primary veins with the midrib, the deeply cleft staminal tube with its lobes very hairy on both sides nearly throughout their length, and the prominently pilose anthers; indeed, it appears that the angle between the midrib and the lateral veins is more acute and the staminal tube is more deeply cleft than in any other species of the genus.

MORACEAE

Malaisia scandens (Lour.) Planch. Ann. Sci. Nat. Bot. (4) 3: 293 (1855)

Caturus scandens Lour. Fl. Cochinch. 613 (1790).

Malaisia tortuosa Blanco Fl. Filip. 789 (1837); Ewart and Davies, loc. cit. 78.

No specimens collected; determinations in the field based on barren plants. It is a common species in eastern Queensland, and has been generally known in Australian literature as *Malaisia tortuosa* Blanco. The generic name was misspelt *Mailaisia* by Ewart and Davies (loc. cit.).

Other species of this family will be discussed elsewhere.

MYRISTICACEAE

Myristica insipida R. Br. Prodr. 400 (1810); Benth. Fl. Aust. 5: 282; Ewart & Davies, loc. cit. 111 (1917)

M. cimicifera Soland. ex R.Br. Prodr. 400 (1810).

M. cimicifera Soland. ex R.Br. var. *insipida* (R.Br.) Warb. Nov. Act. Nat. Cur. 68: 501 (1897).

NORTHERN TERRITORY.—Darwin, in monsoon forest, grey lateritic soil, 8 m, 19.ix.1946, *Blake* 17063—*fr.;* Cannon Hill, about 12° 24′ S., 132° 55′ E., in monsoon forest at base of cliffs, 2.x.1946, *Blake* 17118—*fr;* E. of Fog Bay, 12° 50′-51′ S., 130° 26′-27′ E., in small patch of monsoon forest on laterite, about 30 m, 10.viii.1946, *Blake* 16762—*fr.;* near Alligator Point, Daly R., 13° 26′-29′ S., 130° 26′-27′ E., common understorey tree in riverain closed forest, 5 m, 28.vii.1946, *Blake* 16648—*fl.*

A tree 6-13 m high, rather widely spread in monsoon forests and fringing forests in Northern Australia, with brown, more or less scaly to finely fissured bark exuding a reddish sap when cut, leaves with a glossy, dark green upper surface and whitish beneath, cream dioecious flowers, green fruits, and brown seeds with a red aril that has a faint spicy taste.

Warburg (loc. cit.) took up the name *Myristica cimicifera* Soland. ex R. Br. on the grounds that it was proposed earlier than *Myristica insipida.* However, both names were published simultaneously. Bentham was the first to treat them as synonymous, and his choice of *M. insipida* must be followed. *Blake* 16648 and parts of 17063 closely match an isotype; otherwise the specimens cited have larger leaves, up to 24 by 8 cm on pieces of 16762.

Horsfieldia australiana S. T. Blake; sp. nov., affinis *H. bivalvi* (Hook.f.) Merr., a qua foliis nec caudatis nec acute acuminatis nervis minus curvatis, floribus orbicularibus differt

Arbor dioeca circa 12 m alta, cortice fusco-cinereo rimoso plus minusve squamoso obtecta, basi anteridibus parvis praedita. Ramuli primo leviter compressi minutissimeque puberuli, mox teretes glabri, tandem brunnei rimosi. Folia in sicco fuscescentia haud nitida, subtus pallidiora, chartacea; petiolus 5-10 mm longus; lamina elliptica, apice anguste obtusa vel obtuse subacuminata, basi acuta in petiolum plus minusve decurrens, pro more 17-23 cm longa et 5-7 cm lata (3-3½-plo longa quam lata), marginibus omnino curvis haud parallelis; nervi sursum plus minusve impressi, obscuri; costa media subtus valde prominens, angusta; nervi laterales utrinsecus costam circa 12-15, rectiusculi, prope margines arcuatim conjuncti, subtus paulo conspicui. Inflorescentiae ex axillis foliorum vivorum vel delapsorum orientes, plus minusve pyramidales, floribus glomeratis densiflorae, bracteis exceptis glabrae vel fere glabrae; bracteae plus minusve obovatae, concavae, pubescentes, 1.5-3 mm longae, usque ad 2.4 mm latae; pedunculi circa 1-1.5 mm crassi; pedicelli 0.5-1.5 mm longi. Inflorescentia mascula circa 3-6 cm longa, pedicellis filiformibus; flores rotundati haud truncati, lateraliter compressi, 2-2.3 mm longi, 2.2-2.4 mm lati; perianthium 2-lobum circum ad medium fissum; columna staminalis fere sessilis; antherae circa 12, apice inflexae. Inflorescentia feminea pro more 1.5-2.5 cm longa pedicellis quam in inflorescentia mascula crassioribus; flores fere globosi, brevius bilobi, 2.5-3 mm diametientes; ovarium ovoideum glabrum; stigma sessile. Fructus haud visus.

A dioecious tree about 12 m high, slightly buttressed at the base, with brown, closely fissured, rather thickly scaly bark, yellowish when cut, with watery sap turning red on exposure to the air. Branchlets at first slightly compressed and very minutely puberulous, soon becoming terete and glabrous, at length brown and finely fissured. Leaves glossy green above when fresh but dull and brownish on the dried specimens, paler beneath, chartaceous; petioles 5-10 mm long; blades elliptic with the margins curved throughout (i.e. the margins nowhere parallel), narrowly obtuse or obtusely subacuminate, acute at the base and more or less decurrent into the petiole, 3-3½ times as long as wide, usually 17-23 cm long and 5-7 cm wide; veins more or less impressed on the upper surface, obscure; midrib strongly raised on the lower surface, narrow; lateral veins about 12-15 on each side of the midrib, nearly straight, curved near the margin and there uniting with one another, slightly conspicuous on the lower surface. Inflorescences in the axils of living or (on older parts of the branches) fallen leaves, more or less pyramidal, dense-flowered with the flowers clustered, glabrous or nearly so except for the pubescent, more or less obovate, concave bracts 1.5-3 mm long and up to 2.4 mm wide; peduncles about 1-1.5 mm thick; pedicels 0.5-1.5 mm long. Male inflorescence about 3-6 cm long with filiform pedicels; flowers rounded, laterally compressed, 2-2.3 mm long, 2.2-2.4 mm wide; perianth 2-lobed to about the middle; staminal column nearly sessile; anthers about 12, inflexed at the tips. Female inflorescence usually 1.5-2.5 cm long; pedicels thicker than in the male inflorescence; flowers nearly globular, shortly bilobed, 2.5-3 mm in diameter; ovary ovoid, glabrous; fruit not seen.

NORTHERN TERRITORY.—About 12° 30′ S., 131° 35′-40′ E., tiny patch of monsoon forest on sandy soil, 16.ix.1946, *Blake* 17019 (dioecious, slightly buttressed tree of 12 m with brown, closely fissured rather thickly scaly bark, yellowish when cut, with watery sap turning red on exposure to air; glossy green leaves dull pallid beneath; yellow to orange flowers, males (only) with spicy scent)—male and female *fl.*

Horsfieldia has not previously been reported from Australia, except for the remark in Aust. J. Bot. **1**: 331 (1953). More than 60 species are known from Malaysia, Burma, and the neighbouring parts of India. The genus is distinguished from *Myristica* particularly by the entire aril and ebracteolate flowers which are also smaller, more rounded in outline (neither urceolate nor campanulate), and more numerous in looser paniculate inflorescences; to a large degree the leaves lack the extreme paleness of the lower surface so characteristic of *Myristica*. The fruits and seeds of the Australian species are unknown, but the other features agree with *Horsfieldia*. Its most outstanding characters are the almost entire lack of indumentum, the elliptic obtuse scarcely acuminate, shortly petiolate leaves with nearly straight veins, and rounded 2-lobed flowers (Plate 5). Its nearest ally appears to be the rather widely spread *H. bivalvis* (Hook.f.) Merr. (*H. globularia* Warb.; *Myristica globularia* Bl. non Lam.), from which it differs in the leaves neither caudate nor acutely acuminate with less curved veins and rounded (neither truncate nor transversely oblong) smaller flowers. The collection cited consists of 12 leafy shoots bearing inflorescences, and some detached inflorescences. They represent both sexes and were taken from neighbouring trees.

NYMPHAEACEAE

Nelumbo nucifera Gaertn. Fruct. **1**: 73, *t.* 19, *f.* 2 (1788); Ewart & Davies, loc. cit. 111

Nymphaea nelumbo L. Sp. Pl. 511 (1753).

Nelumbium speciosum Willd. Sp. Pl. **2**: 1258 (1799); Benth. op. cit. **1**: 62 (1863).

Nelumbium nelumbo (L.) Druce, Bot. Exch. Club Brit. Isles 1913, **3**: 421 (1914).

NORTHERN TERRITORY.—In Wild Boar Lagoon, 12° 39′ S., 131° 36′ E., common, 16.ix.1946, *Blake* 17028 (tuberous, rooting at bottom of lagoon; leaves and peduncles erect, standing 30-60 cm above water-level; green leaves, paler beneath; pink petals; yellow stamens)—detached leaves and *fl.*; South Alligator R., 13° 5′ S., 132° 18′ E., deeper parts of drying-out lagoon, 30.ix.1946, *Blake* 17097 (leaves and peduncles together, erect, up to 1.2 m high; rather olive green leaves, paler beneath; pink petals, whitish near base; yellow stamens)—detached leaves and *fl.*

The name *Nelumbium* Juss. Gen. 68 (1789) has been in very general use for this genus, although *Nelumbo* Adans. has clear priority. I have not seen Adanson's original publication of the name in Fam. Pl. **1**: 73 (1763), but Gaertner published a satisfactory description in the year previous to the appearance of Jussieu's work (Plate 6, Fig. 1).

Nymphaea gigantea Hook. Bot. Mag. *t.* 4647 (1852)

It is presumed that the large-flowered *Nymphaea* common in the area with either white or blue flowers belongs to this widely spread Australian species, which is closely allied to *N. stellata* Willd. (Plate 6, Fig. 1).

PALMAE

Livistona humilis R. Br. Prodr. 268 (1810); Benth. op. cit. **7**: 146 (1878);

Beccari & Martelli, Ann. Roy. Bot. Gard. Calcutta **13**: 95, pl. 7, figs. 3 and 3A, pl. 51

Livistona leichhardtii F. Muell. Fragm. 5: 49 (1865), *nomen nudum;* Fragm. 8: 221 (1874).

NORTHERN TERRITORY.—Near Grove Hill, about 13° 28′ S., 131° 35′ E., in *Eucalyptus* forest on sandy or stony soil, about 90-105 m, 6.vii.1946, *Blake* 16347 (slender, unbranched palm up to 6 m; leaves numerous, oblique, green; inflorescence 1.2-2.5 m long; peduncle short or up to 1.8 m; flowers yellow, scented; fruit green to black)—*fl., fr.*

Rather common in the greater part of the Katherine-Darwin area, sometimes as an understorey tree in *Eucalyptus* forest, sometimes forming open scrubs. It is also known from Queensland and a variety has been described from southern Netherlands New Guinea. It is rather easily distinguished by reason of its slender trunk rarely exceeding 4 m in height (Plate 6, Fig. 2), relatively small and stiff leaves with the petioles strongly armed nearly throughout and the prominently veined blades deeply divided into relatively few, stiff, shortly to rather deeply bifid segments, very small flowers clustered on the pubescent branches of the inflorescence, and obovoid to pyriform fruits of medium size with more or less oblong-ellipsoid seeds nearly twice as long as wide with the integument intruded to about the middle of the albumen and the embryo about the middle of the side opposite the chalaza.

Ewart and Davies (loc. cit. 64) cited *L. humilis* as a synonym of *L. mariae* F. Muell. But *L. mariae* was not published until 1878, and in any case this name refers to an entirely different palm of coarser habit that has larger leaves with more numerous and more deeply divided segments which droop for some considerable distance from the tip, and less distinct veins, globular fruits, and globular seeds with comparatively less albumen because of the greater intrusion of the integument.

Livistona benthamii F. M. Bail. Qd. Fl. 5: 1683 (1902) ; Beccari & Martelli, Ann. Roy. Bot. Gard. Calcutta **13**: 84, pl. 6, fig. 4

Livistona humilis R.Br. var. . . . F. M. Bail. Qd. Agric. J. 2: 130 (1898).

NORTHERN TERRITORY.—About S. of "Koolpinyah", 12° 32′ S., 131° 14′ E., associated with *Melaleuca* sp. along shallow drainage channel, 10.ix.1946, *Blake* 16967 (palm with simple, erect trunk, 12-15 m high; numerous, more or less shining green leaves, petiole 1.2-1.5 m long, its edges strongly armed towards base, slightly so at top, smooth in middle; inflorescence intrafoliar, pendulous, about 1.2 m long)—*fr.* (immature).

New for the Northern Territory; previously known only from the neighbourhood of Cape York, Queensland. Except for the slightly smaller leaves, these specimens match the type exactly. It is readily distinguished from *L. humilis* by its stouter trunk attaining a much greater height, much more numerous and larger leaves of thinner texture with long-drooping segments, and much smaller fruits narrowed to the base (Plate 6, Figs. 3 and 4). It was noted only to the E. and SE. of Darwin, in tall *Melaleuca* forest or on river banks.

In the protologue Bailey cited only one collection (Somerset, *Frank L. Jardine*), but quoted a native name and native uses from Roth. This native name "dre-amberi" appears on the field label to *Roth* 227 in herb. Brisbane (dré-am-be-ri) which consists of 3 leaves with shortly bifid segments and 3 partial inflorescences with a very few immature, small, globular fruits; it evidently represents a species distinct from *L. benthamii.*

Two other species have been recorded from the northern part of the Northern Territory. *L. inerme* R. Br. appears to be represented only by the type collection from islands of the Gulf of Carpentaria (? Sir Edward Pellew's Group) and was originally diagnosed from *L. humilis* by the unarmed petiole. A small-leaved slender palm with smooth petioles probably belonging to this species was observed in 1946 about SE. of the junction of the McKinlay and Mary Rivers, but as the plants were sterile, no specimens were collected. Beccari (Webbia 5: 18 (1920)) described *L. holtzei* from sterile material collected by N. Holtze at "Glencoe", relying on Holtze's statement that the fruit was globular and that the plant differed from *L. humilis* (Beccari and Martelli, loc. cit. 86-7). All the palms I saw in the neighbourhood of "Glencoe" appeared to be *L. humilis,* and it is from this general locality that the specimens cited above were collected.

Ewart and Davies (loc. cit.) recorded 5 palms from the Northern Territory, one erroneously (*L. alfredii* F. Muell.). The following species have now been recorded from the area:

Corypha elata Roxb. Fl. Ind. 2: 176 (1832); C. T. White, Proc. Roy. Soc. Qd. **61**: 55 (1950).

Livistona humilis R. Br. (see above).

Livistona inermis R. Br. Prodr. 268 (1810); Benth. op. cit. **7**: **146** (1878); Ewart & Davies, loc. cit.

Livistona benthamii F. M. Bail. (see above).

Livistona holtzei Becc. (see above).

Livistona mariae F. Muell. Fragm. 8: 283 (1874), *nomen;* in Giles, Geogr. Travels in Centr. Aust. 222 (1875), *nomen;* Fragm. **11**: 54 (1878); Vict. Nat. **9**: 112 (1892)

Kentia ramsayi (Becc.) Becc. Webbia **4**: 148 (1913).

Gulubia ramsayi Becc. Webbia **3**: 159 (1910).

Carpentaria acuminata (Wendl. & Drude) Becc. Ann. Jard. Bot. Buitenz. 2: 128 (1885).

Kentia acuminata Wendl. & Drude, Linnaea **39**: 207 (1875); Benth. op. cit. **7**: (1878); Ewart & Davies, loc. cit. 64.

Hydriastele wendlandiana (F. Muell.) Wendl. & Drude, Linnaea **39**: 209 (1875)

Kentia wendlandiana F. Muell. Fragm. 7: 102 (1870); Benth. op. cit. 7: 138 (1878); Ewart & Davies, loc. cit. 64.

Ptychosperma wendlandiana (F. Muell.) Burret, Notizbl. Bot. Gart. Berl. **10**: 205 (1927), *quoad basonym.*

Actinophloeus bleeseri Burret, Repert. Nov. Spec. Regn. Veg. 24: 266 (1928), *in nota.*

Ptychosperma bleeseri Burret, loc. cit.

PANDANACEAE

This family has been intensively studied by O. Warburg and U. Martelli. Warburg's work on the family was published as Das Pflanzenreich 3 (IV: 9) (1900). Martelli's work was published in a number of papers, the outstanding ones on *Pandanus* (the only genus known from the Northern Territory) being the profusely illustrated "Enumerazione delle Pandanaceae" in Webbia 4: 1-104 and 43 plates (1913) and "Le specie e varietà nuove de *Pandanus*" in Webbia 4: 399-435 (1914); other papers have appeared since, some of them dealing with Australian species.

Our knowledge of the Australian forms is far from satisfactory. About 12 species have been recorded from the continent, chiefly from Queensland, but many of the records are based on solitary collections. Adequate collections are not easy to prepare, and much of the material consists merely of loose portions of the general infructescence, i.e. of loose phalanges (groups of connate drupes) or loose drupes. It is probable that there is much greater individual variation than is usually admitted.

Pandanus spiralis R. Br. Prodr. 341 (1810)

NORTHERN TERRITORY.—Near "Koolpinyah", 12° 25′ S., 131° 13′ E., forming small or large communities near edge of swampy grassland, about 9 m, 10.ix.1946, *Blake* 16964 (slender tree to 6 m high; few branches; spirally tufted leaves at ends of branches; pendulous syncarps; red phalanges)—*leaves, phalanges;* near Hot Springs, Douglas R., about 13° 46′ S., 131° 27′ E., common in flat drainage channels, 70 m, 11.vii.1946, *Blake* 16433 (tree, often gregarious, to 9 m high; no prop roots; trunk with loosely spiral shallow furrow and few short erect processes, erect or shortly decumbent at base and there rooting; few branches; numerous slightly glaucous leaves about 2 m long in dense spiral terminal tufts, bent downwards 1/3 from base; pendulous, orange subglobular syncarp about 30 cm diam.)—*leaves, phalanges.*

A common species, widely spread on seepage slopes, the margins of drainage channels, the banks of small watercourses, and other similar habitats; it has not been observed at the margins of permanent streams nor on the coastal dunes. Its outstanding characters are the absence of aerial roots and the smooth-sided phalanges formed of numerous drupes not pyramidal at the apex, so that the top of the phalange is tessellated and nearly flat (Plate 7, Figs. 1 and 2). These characters (except the smooth sides) were described by Brown (loc. cit.) to distinguish the species from *P. pedunculatus* R. Br., which produces abundant aerial roots and drupes with pyramidal-conical tops. The same characters distinguish *P. spiralis* from the widely spread *P. odoratissimus* L.f. (= *P. tectorius* Solander ex Parkinson), under which name the species was described by Bentham, op. cit. 7: 148-9 (1878) and recorded by Ewart and Davies, loc. cit. 20. *P. tectorius* is a variable species, and in some forms the phalanges tend to resemble those of *P. spiralis;* in others the phalanges tend to resemble those of *P. pedunculatus*. Both *P. pedunculatus* and *P. tectorius* occur on the eastern coast of Queensland, the latter in the form described by Martelli as *P. tectorius* var. *australianus* Martelli.

The specimens cited above do not quite match each other, but they agree with Brown's diagnosis and it is difficult to distinguish either from specimens at Brisbane determined by Martelli or from Martelli's figure in Webbia 4: *t.* 13, *f.* 1-2 drawn from Hulse's collection from Escape Cliffs, cited by Bentham.

Pandanus basedowii C. H. Wright, Kew Bull. **1930: 158, pl. 6** (1930)

NORTHERN TERRITORY.—Cannon Hill, about 12° 24′ S., 132° 55′ E., exposed rocky slopes, on cliffs, 2.x.1946, *Blake* 17134 (small branched tree up to 5 m high with prop roots; leaves in spiral tufts at end of branches, about 0.5 m long; syncarp globular, about 20 cm diam. The only syncarp seen had 13 phalanges)—*leaves, broken up syncarp.*

This species was described from specimens collected by Basedow on "high tablelands of Arnhem Land, c. 310 m. alt." A photograph published with the original description shows the characteristic habit of the plant, with its prop-roots and widely spreading, nearly horizontal branches with relatively short leaves. My specimens appear to represent only the second collection of this species, and they came from cliffs near the NE. edge of the Arnhem Land plateau (Plate 7, Fig. 4). They differ from the original description in the shorter phalanges, 5-5.5 cm instead of 7 cm long and are 4-5.5 cm wide. Of the 13 phalanges in the solitary syncarp collected, 5 are composed of a single drupe, and 8 are formed of 2 drupes. In the protologue, Wright remarked that most species of the genus inhabit sea-shores, but that *P. basedowii* was "remarkable for growing on dry rocky barren surfaces in the interior of Arnhem Land at an altitude of about 1000 ft." and that *P. monticola* F. Muell. grows in similar situations in Queensland. It should be noted that a large proportion of the species of the genus does not inhabit sea-shores, and that *P. monticola* is found in the rain-forests of NE. Queensland, in a very different habitat from that of *P. basedowii.*

The species is well distinguished from the other Australian species by the paired or solitary, large, very light drupes.

Pandanus aquaticus F. Muell. Kew J. Bot. 8: 324 (1856), *nomen provisorium et seminudum,* Fragm. 5: 40 (1865); Benth. op. cit. 7: 149 (1878); Ewart & Davies, loc. cit. 20 (1917); Warburg, loc. cit., 85 (1900); Martelli, Webbia 4: 6 (1913)

P. delestangii Martelli, Proc. Roy. Soc. Qd. 38: 57, pl. 11 (1927) (*"de Lestangii"* and *"deLestangii"*): *syn. nov.*

NORTHERN TERRITORY.—Daly R., about 14° 5′ S., 131° 15′ E., close to edge of water (dry season), 1.vii.1946, *Blake* 16256 (about 6 m high; stems clustered, branched in upper part, with short erect processes; mostly no prop-roots in evidence; dull green leaves tufted at ends of branches, erect to drooping; drupes picked up from the ground) —*leaves, drupes.* Katherine, sandy bank of Katherine R., about 100 m, 23.vi.1946, *Blake* 16085 (monoecious tree about 6 m high with single trunk and few branches all covered with short erect processes; leaves tufted at end of branches, about 2 m long;

syncarp pendulous, globular, about 15 cm dia.; male inflorescence below the leaves)—*leaves, broken up syncarp.*

The species is confined to the banks of perennial streams in the northern part of the Northern Territory and the adjacent parts of NW. Queensland. The eastern limit appears to be the Gregory-Albert river-system.

Mueller's first reference to the species reads ". . . a species with free drupes, which, if distinct from the Indian kinds, may be called *P. aquaticus*, as it indicates, and lives permanently in water, and has been introduced as "Water Pandanus" in Dr. Leichhardt's work."* The species and name were definitely accepted in 1865, and the remarks given are sufficient to validate the name. Although Mueller mentioned the solitary drupes, apparently only leaves and a male inflorescence were sent to Bentham. No specimen appears to have been seen by Warburg or Martelli.

Later, Martelli (loc. cit.) described *P. delestangii* from fruiting material collected in February 1925, by A. de Lestang in NW. Queensland "under palms along perennial streams about 200 miles south-west of Burketown." Part of the type collection is at Brisbane. A later collection by de Lestang from the same area consists of leaves, a male inflorescence, and fragments of the female inflorescence. *Blake* 8694 from Riversleigh, Gregory R., near the type locality, is very like the type, but has rather larger drupes and closely resembles the specimens from the Northern Territory cited above. Therefore it seems necessary to treat *P. delestangii* as a synonym of *P. aquaticus*. The species is well distinguished from the other Australian species by the narrow drupes about 3.5-4.5 cm long and only 0.9-1.3 cm wide. At maturity nearly all fall singly, though some are united in pairs or in threes in uniseriate phalanges. The union may be complete or only partial, and then in various degrees.

In the protologue of *P. delestangii*, Martelli somewhat doubtfully referred the species to sect. *Hombronia* because of the uniseriate arrangement of the phalanges when the drupes were united, but pointed out that the absence of male flowers did not allow its true position to be determined. But united drupes appear to be exceptional, and the arrangement of the anthers is quite different from that of sect. *Hombronia*, in which they are clustered beneath a peltate apex of the staminal column. In *P. aquaticus* the anthers are loosely clustered towards the end of the column, with the upper part of the filaments free. This arrangement is found in sect. *Keura* and in sect. *Rykia*, while the narrow, usually solitary drupes also agree with *Rykia*, although the style and stigmas are often shorter than is usual in this group. To judge from the key, descriptions, and figures of Warburg and the figures of Martelli, *P. aquaticus* resembles the southern Indian *P. canaranus* Warb. more closely than any other species. Its habit is shown in Plate 7, Figure 3.

* Mueller's reference appears to be to Leichhardt: Journal of an Overland Expedition to Port Essington, pp. 390, 421, 442 (London, 1847).

Two other species have been reported from the Northern Territory, both belonging in sect. *Keura*. In Proc. Roy. Soc. Qd. 45: 24 (1934) Martelli recorded *P. whitei* Martelli from near Darwin on the basis of material collected in January 1927, by C. E. F. Allen; part of this collection is at Brisbane and it bears an earlier, unpublished name of Martelli's. *P. whitei* is fairly common in NE. Queensland; it resembles *P. spiralis* in habit, but the drupes have a prominently pyramidal-conical apex and rather deep longitudinal furrows on all free surfaces. Warburg (loc. cit. 46) recorded *P. solms-laubachii* F. Muell. from "North Australia" on the basis of *Schultz* 613, quoted by Bentham under *P. odoratissimus* with Port Darwin as the locality. *P. solms-laubachii* resembles *P. whitei* in having drupes with furrowed sides and pyramidal tops, but the drupes are narrower, the stigma is lateral rather than terminal, and the leaves are very much longer, a distinction very evident in the field. I have not seen Schultz's specimen, which may be referable to *P. whitei.*

The species of which I have seen specimens from the Northern Territory may be distinguished by the following key:

Drupes falling singly or united in groups (phalanges) of 2 or 3:
  Drupes about 3.5-4.5 cm long and only 0.9-1.3 cm wide; plant of the edge of perennial streams with few, if any, prop-roots .. .. *P. aquaticus*
  Drupes about 5-7 cm long and 4.5-5.5 cm wide; plant of barren sandstone cliffs and tablelands with numerous prop-roots .. .. *P. basedowii*
Drupes united in groups (phalanges) of 9 or more; prop-roots absent:
  Apex of drupes low and flattened; sides not furrowed .. .. *P. spiralis*
  Apex of drupes more or less conical or pyramidal; all free sides with prominent longitudinal furrows .. .. *P. whitei*

PASSIFLORACEAE

Passiflora foetida L. Sp. Pl. 959 (1753)

NORTHERN TERRITORY.—Darwin, disturbed stony ground, open *Eucalyptus* forest, about 15 m, 29.x.1946, *Blake* 17331 (trailing and climbing tufted stems; rather olive green leaves; dirty white corolla; purplish corona)—*fl.*

Not previously recorded for the Northern Territory; a native of tropical America, now pantropic in distribution.

PITTOSPORACEAE

Pittosporum melanospermum F. Muell. Fragm. 1: 70 (1859); Benth. op. cit. 1: 111 (1863); Ewart & Davies, loc. cit. 117

NORTHERN TERRITORY.—About SW. of Katherine, about 14° 45′ S., 131° 47′ E., river levee, mixed open forest, about 95 m, 11.x.1946, *Blake* 17199 (bushy-crowned, evergreen (?) tree of 6 m; grey, closely fissured, more or less tessellately scaly bark; rather yellowish leaves; orange fruits; black seeds)—*fr.*

Northern Territory, Western Australia. This is the first specific locality for the Northern Territory, the only previously recorded one being "low rocky hills between Victoria River and Gulf of Carpentaria." The other locality cited by Ewart and Davies, loc. cit., is in Western Australia (York Sound).

RHAMNACEAE

Ziziphus quadrilocularis F. Muell. Fragm. 3: 57 (1862); Benth. op. cit. 1: 412 (1863); Ewart & Davies, loc. cit. 176 (*"Zizyphus"*)

NORTHERN TERRITORY.—Flora R., near junction with Katherine R., fringing forest on steep bank, about 98 m, 16.x.1946, *Blake* 17245 (tree, 6-7.5 m high; pale green, smooth bark decorticating in dull grey flakes like some eucalypts; spreading branches; green leaves, whitish beneath; dull purple fruits; young plants thorny)—*fr., juvenile shoots.*

Only the type collection (Upper Victoria River, *Mueller*) has been reported previously; this was described as having the fruits usually 4-celled, rarely 3-celled, but the fruits of the specimens cited above are mostly 3-celled, rarely 4-celled. Young plants have stipular spines up to 10 mm long, but the branches of older plants are unarmed. The bark, described in the field notes cited above, is very characteristic. The generic name should be spelt *Ziziphus*, not *Zizyphus* (Sprague, Kew Bull. **1929**: 51 (1929)).

Colubrina asiatica (L.) Brongn. Ann. Sci. Nat. (I) **10**: 369 (1827); Benth. op. cit. **1**: 413 (1863)

Ceanothus asiaticus L. Sp. Pl. 196 (1753).

NORTHERN TERRITORY.—Darwin, on low sand dune behind mangroves, 19.ix.1946, *Blake* 17053 (shrubby small tree; pale green leaves, paler beneath)—*fr.*

New for the Northern Territory; previously known from Queensland, parts of Malaysia, and Polynesia. A plant of the sea-shore and borders of tidal streams.

Alphitonia excelsa (Fenzl) Benth. Fl. Aust. **1**: 414 (1863); Ewart & Davies, loc. cit. 176

Colubrina excelsa Fenzl, Enum, Pl. Huegel. 20 (1837).

NORTHERN TERRITORY.—About SW. of Katherine, about 14° 40′ S., 131° 49′ E., mixed open forest, sandy soil, 94 m, 11.x.1946, *Blake* 17200 (tree of 6 m; grey, hard, rather scaly-looking, fissured bark; rather yellowish green leaves white beneath; black fruit)—*fr.*

Widely spread in the *Eucalyptus* forests of the Northern Territory and Queensland; the northern trees have much rougher bark than the southern ones, which commonly have smooth or nearly smooth, whitish bark. The authorship of the combination under *Alphitonia* has always been quoted as "Reissek ex Endl. Gen. 1098," but here is found only the generic description of *Alphitonia* followed by the paragraph: Alphitonia Reissek *msc.* Colubrina excelsa Fenzl *in Enum. pl. Hugel.* 20 *in adn.*

RHIZOPHORACEAE

Rhizophora mucronata Lam. Encycl. **6**: 189 (1804); Benth. op. cit. **2**: 493 (1864); Ewart & Davies, loc. cit. 199

NORTHERN TERRITORY.—Darwin, mangrove forest on shallow mud overlying laterite, dominant species, particularly towards the sea, 19.ix.1946, *Blake* 17049 (tree, 6-9 m high, with numerous arching branched roots from trunk and lower branches; rather dense green crown; green leaves, paler beneath; cream sepals, white petals; yellow anthers)—*fl.*

Widely spread on the tropical shores of the Old World, extending in eastern Australia as far south as 28° S., but this seems to be only the second definite record of the species from the Northern Territory.

Ceriops tagal (Perr.) C. B. Rob. Philip. J. Sci. 3: Bot. 306 (1908)

Rhizophora tagal Perr. Mém. Soc. Linn. Paris 3: 138 (1824).

Rhizophora timoriensis DC. Prodr. 3: 32 (1828).

Ceriops candolleana Arn. Ann. Nat. Hist. 1: 364 (1838); Benth. op. cit. 2: 494 (1864); Ewart & Davies, loc. cit. 199 (1917).

Ceriops timoriensis (DC.) Domin, Bibl. Bot. 89: 444 (1928).

NORTHERN TERRITORY.—Darwin, mangrove forest on shallow mud overlying laterite, occasional near landward edge, 19.ix.1946, *Blake* 17050 (bushy-crowned tree, 4.5-6 m high; fluted, slightly flanged trunk; yellowish grey, coarsely lenticellate, sometimes flaky bark; green leaves; reddish sepals; white petals)—*fl., young fr.*

Bruguiera parviflora (Roxb.) Wight & Arnott, Prodr. 311 (1834); C. T. White, Proc. Roy. Soc. Qd. **61**: 58 (1950)

Rhizophora parviflora Roxb. Fl. Ind. 2: 641 (1832).

NORTHERN TERRITORY.—About 12° 40′ S., and 131° 25′ E., muddy bank of small creek at its junction with Adelaide R., 14.ix.1946, *Blake* 16995 (tree of 6 m, swollen at base, with thick, low knee-roots; green leaves, paler beneath; cream flowers)—*fl.*, immature *fr.*

New for the Northern Territory mainland; known elsewhere from Malaysia, India, north Queensland, New Hebrides, and the Solomon Is.

Carallia brachiata (Lour.) Merr. Philip. J. Sci. 15: 249 (1919)

Diatoma brachiata Lour. Fl. Cochinch. 296 (1790).

Petalotoma brachiata (Lour.) DC. Prodr. 3: 295 (1828).

Carallia integerrima DC. Prodr. 3: 33 (1828); Benth. op. cit. 2: 495 (1864); Ewart & Davies, loc. cit. 199.

NORTHERN TERRITORY.—Rum Jungle, 13° 1′ S., 131° 0′ E., in monsoon forest, alt. about 60 m, 8.viii.1946, *Blake* 16722 (tree, 4.5-6 m high; irregular, not buttressed trunk with indistinct transverse ridges; grey, hard, sparsely fissured bark; dark shining green leaves, paler beneath; whitish petals; green to red fruit)—*fl., fr.;* near Hot Springs, Douglas R., about 13° 46′ S., 131° 27′ E., in fringing forest, 70 m, 10.vii.1946, *Blake* 16428 (small tree of 4.5 m; grey, furrowed, corky bark; shining green leaves paler beneath; greenish white flowers)—*fl.;* S. of mouth of Daly R., about 13° 45′ S., 130° 17′ E., shady creek bank, 21.vii.1946, *Blake* 16538 (shrub about 2 m high; shining green leaves; whitish petals)—*fl.*

Widely spread from SE. Asia to Northern Australia in rain forest and monsoon forest.

RUTACEAE

Boronia lanceolata F. Muell. Fragm. 1: 66 (1859); Benth. op. cit. 1: 314 (1863); Ewart & Davies, loc. cit. 157

NORTHERN TERRITORY.—Near Edith Falls, 14° 10′ S., 132° 12′ E., narrow belt of fringing forest on damp shaded river bank, 116 m, 21.x.1946, *Blake* 17273 (slender shrub of 2 m; somewhat olive green leaves, more or less glaucous beneath; greenish white to pale pink flowers)—*fl.*

Northern Territory, north-western Queensland.

Micromelum minutum (Forst. f.) Seem. Mission Fiji 434 (1862)

Limonia minuta Forst. f. Prodr. 33 (1786).

Micromelum pubescens Bl. Bijdr. 137 (1825); Benth. op. cit. 1: 368 (1863); Ewart & Davies, loc. cit. 157.

Micromelum glabrescens Benth. Lond. J. Bot. 2: 212 (1843).

NORTHERN TERRITORY.—E. of mouth of Daly R., 13° 24½′ S., 130° 40′ E., in fringing forest along creek, about 60 m, 30.vii.1946, *Blake* 16673 (tree 4.5-7.5 m high; bark creamy grey, smooth except for fine faint fissures and transverse lines; leaves green, paler beneath; fruit orange)—*buds, fr.*

Not uncommon in the fringing forests and monsoon forests ("jungles") in the Darwin-Katherine area. India to China through Malaysia and northern and north-eastern Australia to Polynesia. The extensive synonymy of this variable species is listed by Merrill, Enum. Philip. Flow. Pl. **1**: 335 (1923).

SAPINDACEAE

Cardiospermum halicacabum L. Sp. Pl. 366 (1753); Benth. op. cit. **1**: 453 (1863); Ewart & Davies, loc. cit. 173

NORTHERN TERRITORY.—Daly R., about 13° 45′ S. and 130° 42′ E., in fringing forest, 12 m, 17.vii.1946, *Blake* 16497 (green twiner; white flowers; pale green fruits tinged reddish)—*fl., fr.*

Widely spread in the tropics and subtropics.

Atalaya hemiglauca (F. Muell.) F. Muell. ex Benth. Fl. Aust. **1**: 463 (1863); Ewart & Davies, loc. cit. 174

Thouinia hemiglauca F. Muell. Fragm. 1: 98 (1859).

NORTHERN TERRITORY.—South Alligator R., 13° 5′ S., 132° 18′ E., mixed fringing forest near Coirwong Creek, 30.ix.1946, *Blake* 17103 (tree, 7.5 m high; grey, fissured bark; subglaucous leaves; white flowers)—*fl., fr.;* Katherine, lower flood banks of Katherine R., about 100 m, 7.x.1946, *Blake* 17181 (slender tree, 3-6 m high; grey, scaly-looking bark; open crown of dull green leaves paler beneath; creamy white flowers)—*fl., fr.*

Rather widely spread over chiefly the drier parts of Australia; not previously recorded for the Darwin-Katherine area.

Cupaniopsis anacardioides (A. Rich.) Radlk. Sitzb. Bayer. Acad. **9**: 685 (1879)

Cupania anacardioides A. Rich. Sert. Astrol. 33, *t.*3 (1834); Benth. op. cit. 1: 458 (1863); Ewart & Davies, loc. cit. 174.

Alectryon bleeseri O. Schwarz, Repert. Nov. Spec. Regn. Veg. 24: 87 (1927).

NORTHERN TERRITORY.—E. of Fog Bay, 12° 50′-51′ S., 130° 26′-27′ E., in patch of monsoon forest, shallow lateritic soil, 24 m, 12.viii.1946, *Blake* 16780 (tree of 9 m; irregular, more or less fluted trunk with transverse ridges; grey, finely pustular bark; green leaves, rather paler beneath; cream flowers)—*fl.;* about SSE. of mouth of Daly R., bank of Hermit Creek, 23 m, 25.vii.1946, *Blake* 16625 (tree 6-9 m high; flowers pinkish inside)—*fl.*

Schwarz stated that his species differs from "*A. anacardioides* (A. Rich.) Radlk." in having 8 puberulous anthers. Bentham described

Cupaniopsis anacardioides (as *Cupania anacardioides*) as having 10 stamens; Maiden (For. Fl. N.S.W. **1**: 123 *pl.* 20 (1903)) described the stamens as 10 in number, but his figure shows 8. The specimens cited above agree with Schwarz's description and match material from eastern Queensland. At least the usual number of stamens appears to be 8. Very likely Schwarz's use of *Alectryon* is a slip of the pen for *Cupaniopsis*, since he refers to *A. anacardioides* (A. Rich.) Radlk. in his discussion on the species and Radlkofer never published such a combination.

Dodonaea peduncularis Lindl. in Mitch. Trop. Austr. 361 (1848)

D. peduncularis Lindl. var. *coriacea* Ewart & Davies, loc. cit. 175.

NORTHERN TERRITORY.—Near (E. of) Lake Woods, in *Acacia-Triodia* scrub, 2.xi.1946, *Blake* 17358 (viscid, very glaucous shrub of 1 m)—*fr.;* Tennant Creek, with *Triodia* in mixed open low scrub on flat ground, about 240 m, 17.vi.1946, *Blake* 16009 (green, slightly viscid, bushy shrub of 1 m; fruit reddish brown and green)—*fr.*

The leaves are rather broader than usual in the species, with the margins more distinctly toothed, but intermediate states exist, and there seem to be no good grounds for taxonomic distinction.

Dodonaea physocarpa F. Muell. Kew J. Bot. **9**: 197 (1857), Fragm. **1**: 74 (1859); Benth. op. cit. **1**: 484 (1863); Ewart & Davies, loc. cit. 175

NORTHERN TERRITORY.—O.T. Station, about 16° 38′ S., 135° 8′ E., in very open *Eucalyptus* forest, alt. 180 m, 12.v.1947, *Blake* 17723 (broad bushy shrub about 1 m high; leaves subglaucous; fruit pale greenish to pale brown)—*fr.*

These specimens were collected a long way east from previously recorded localities in the Northern Territory, but the species is widely distributed in northern Queensland.

Distichostemon filamentosus S. Moore, J. Linn. Soc. (Bot.) **45**: 197 (1920)

NORTHERN TERRITORY.—W. of Brocks Creek, 13° 30′ S., 131° 11′ E., open *Eucalyptus* forest, 13.vii.1946, *Blake* 16454 (more or less shrubby, 30-100 cm. high; rather olive green leaves; green fruit with purplish wings)—*fr.*

My specimens agree well enough with Spencer Moore's description, but are in fruit only. The species appears to differ from *D. hispidula* (Endl.) Baill. (*D. phyllopterus* F. Muell.) in the more prominently toothed and commonly more acute leaves of thinner texture with the hairs more or less strictly confined to the margins and to the major nerves on the lower surface and the long filaments. Previously known only from the type, which came from Darwin (Palmerston). Neither collection is very satisfactory.

SONNERATIACEAE

Sonneratia caseolaris (L.) Engl. in Engl. & Prantl, Nat. Pfl.fam. Nachtr. **1**: 261 (1897)

S. alba Sm. in Rees Cycl. **33**: No. 2 (1816); C. T. White, J. Bot., Lond. **64**: 217-8 (1926); O. Schwarz, Repert. Nov. Spec. Regn. Veg. **24**: 88 (1927).

Rhizophora caseolaris L. in Stickm. Herb. Amb. 13 (1754).

NORTHERN TERRITORY.—Point Stephens, Adam Bay, seaward edge of mangroves on shelving, pebbly to muddy beach, 9.ix.1946, *Blake* 16953 (large spreading tree with grey, coarsely flaky bark and prominent stout pneumatophores; rather light green leaves paler beneath; green fruit)—*fr.*

C. T. White (loc. cit.) first recorded this species from Australia; according to an editorial note following his article, specimens collected by R. Brown from Arnhem N. Bay mentioned by Bentham, op. cit. 3: 301 (1867) belong to this species and not to *S. acida* L.f. as suggested by Bentham. Both are wide-ranging species, extending from India to north-east Queensland, and may be distinguished as follows:

Leaves obovate, rounded; fruiting calyx obconic, more or less ribbed; flowers reddish .. .. *S. caseolaris*

Leaves oblong to elliptic-oblong, somewhat pointed; fruiting calyx short and broad; flowers white .. .. *S. acida*

S. acida is not yet certainly known from the Northern Territory, for the record of this species by Ewart and Davies (loc. cit. 199) copied from Bentham (loc. cit.) is not localized and only fragmentary material seems to have been collected (cf. Bentham, loc. cit.).

SPHENOCLEACEAE

Sphenoclea zeylanica Gaertn. Fruct. **1**: 113, *t.* 24, *f.* 5 (1788)

NORTHERN TERRITORY.—Adelaide R., 12° 39′ S., 131° 20′ E., dried-out depressions, about 6 m, 11.ix.1946, *Blake* 16976 (stout annual, 30-60 cm high; pale green, somewhat succulent stems; dull green leaves, paler beneath; pale green inflorescence; white corolla)—*fl., fr.* QUEENSLAND.—Normanton, depression in flood plain, light grey clay loam, just above sea-level, 19.v.1935, *Blake* 9016 (erect, more or less branched green annual; calyx green, finally pallid; corolla white)—*fl., fr.*

Family new for Australia; it consists of a single genus of 2 species, one of them nearly pantropical, the other confined to West Africa. The genus has frequently been associated with Campanulaceae, and its habit is that of *Phytolacca.*

EXPLANATION OF PLATES 1-7

PLATE 1

Fig. 1.—*Pistia stratiotes* on lagoon, lower Daly River (*Blake* 16525).

Fig. 2.—*Amorphophallus galbra* (*Blake* 17115).

Fig. 3.—*Cochlospermum fraseri*, leafless and in fruit (foreground), with *Bauhinia cunninghamii* in full leaf (right middle distance) and other trees, SW. of Katherine.

Fig. 4.—*Barringtonia gracilis* near Margaret River (*Blake* 16394; the leaves in the top right-hand corner are of *Melaleuca* sp.).

(Photos: S. T. Blake.)

PLATE 2

Dendrolobium stipatum S. T. Blake from type collection.

(Photo: W. J. Sanderson.)

PLATE 3

Desmodium polyneurum S. T. Blake from type collection.

(Photo: W. J. Sanderson.)

PLATE 4

Vavaea australiana S. T. Blake from type collection.

Fig. 1.—Flowering twig.

Fig. 2.—Detached inflorescence.

Fig. 3.—Open flower.

Fig. 4.—Flower with sepals cut away, corolla removed, and part of the staminal tube cut away to expose pistil.

(Drawing: S. T. Blake; photo: W. J. Sanderson.)

PLATE 5

Horsfieldia australiana S. T. Blake from type collection.

Fig. 1.—Flowering twig of male plant, leaves from beneath.

Fig. 2.—Leaf showing upper surface.

Fig. 3.—Detached female inflorescence.

Fig. 4.—Male flower from the side.

Fig. 5.—Male flower with a perianth segment cut away to show stamens.

Fig. 6.—Female flower from the side.

Fig. 7.—Female flower with a perianth segment cut away to show pistil.

(Drawing: S. T. Blake; photo: W. J. Sanderson.)

PLATE 6

Fig. 1.—*Nymphaea gigantea* (floating leaves) and *Nelumbo nucifera* (leaves raised above the surface, *Blake* 17028), Wild Boar Lagoon.

Fig. 2.—*Livistona humilis* near Grove Hill (*Blake* 16347).

Figs. 3, 4.—*Livistona benthamii* about S. of "Koolpinyah"—Fig. 3, habit; Fig. 4, leaf and inflorescence (*Blake* 16967).

(Photos: 1, C. S. Christian; 2-4, S. T. Blake.)

PLATE 7

Figs. 1, 2.—*Pandanus spiralis* near Hot Springs, Douglas River (*Blake* 16433)—Fig. 1, habit; Fig. 2, syncarp × 0.17.

Fig. 3.—*Pandanus aquaticus* on bank of Daly River (*Blake* 16256).

Fig. 4.—*Pandanus basedowii* on Cannon Hill (*Blake* 17134).

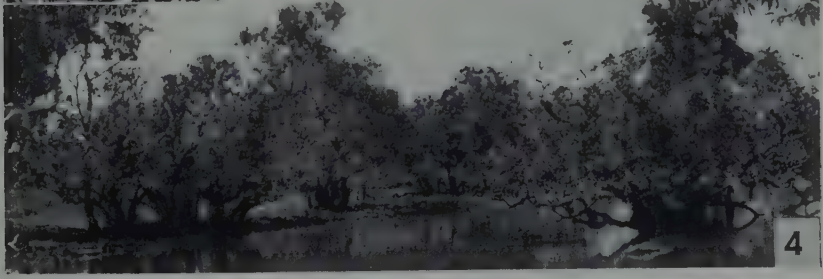
(Photos: S. T. Blake.)

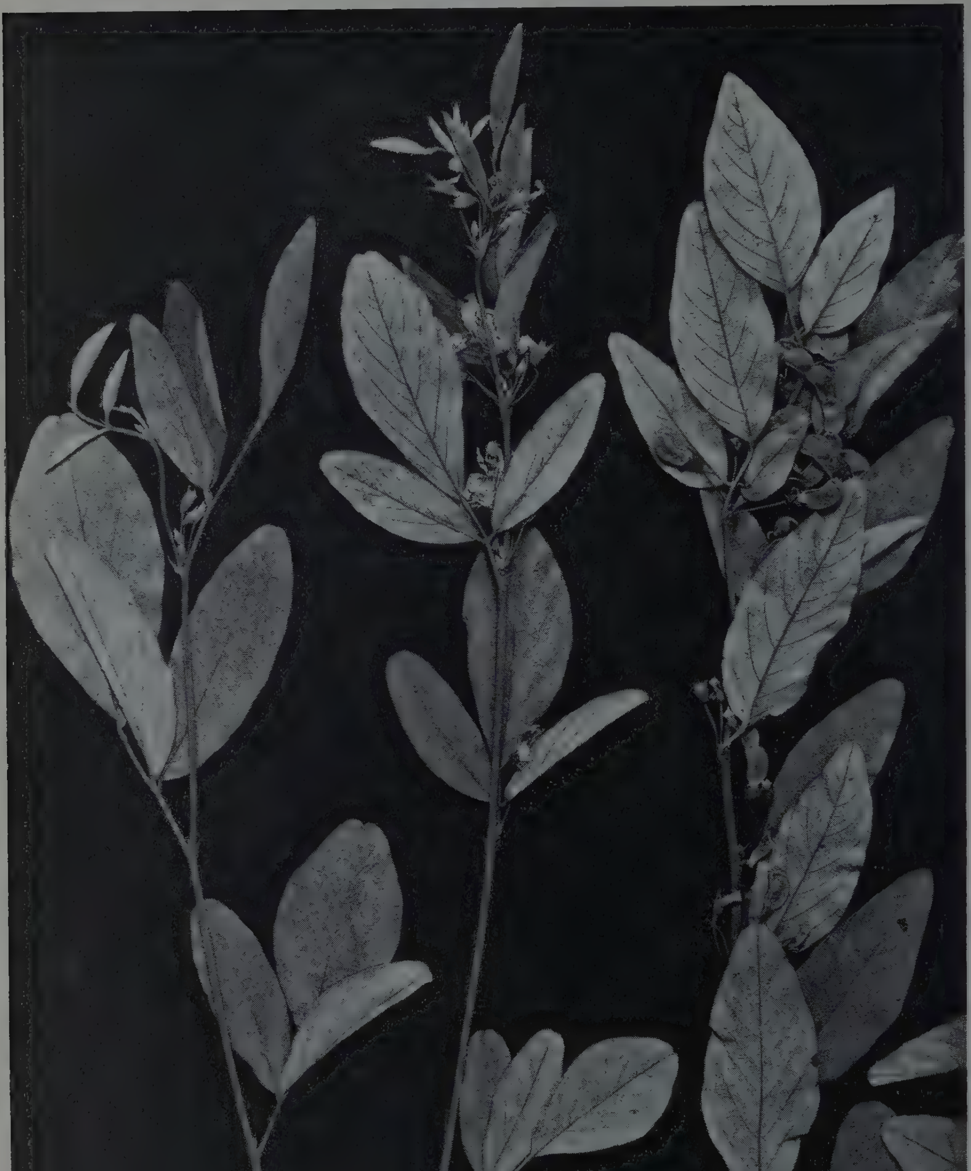
NORTHERN AUSTRALIAN PLANTS

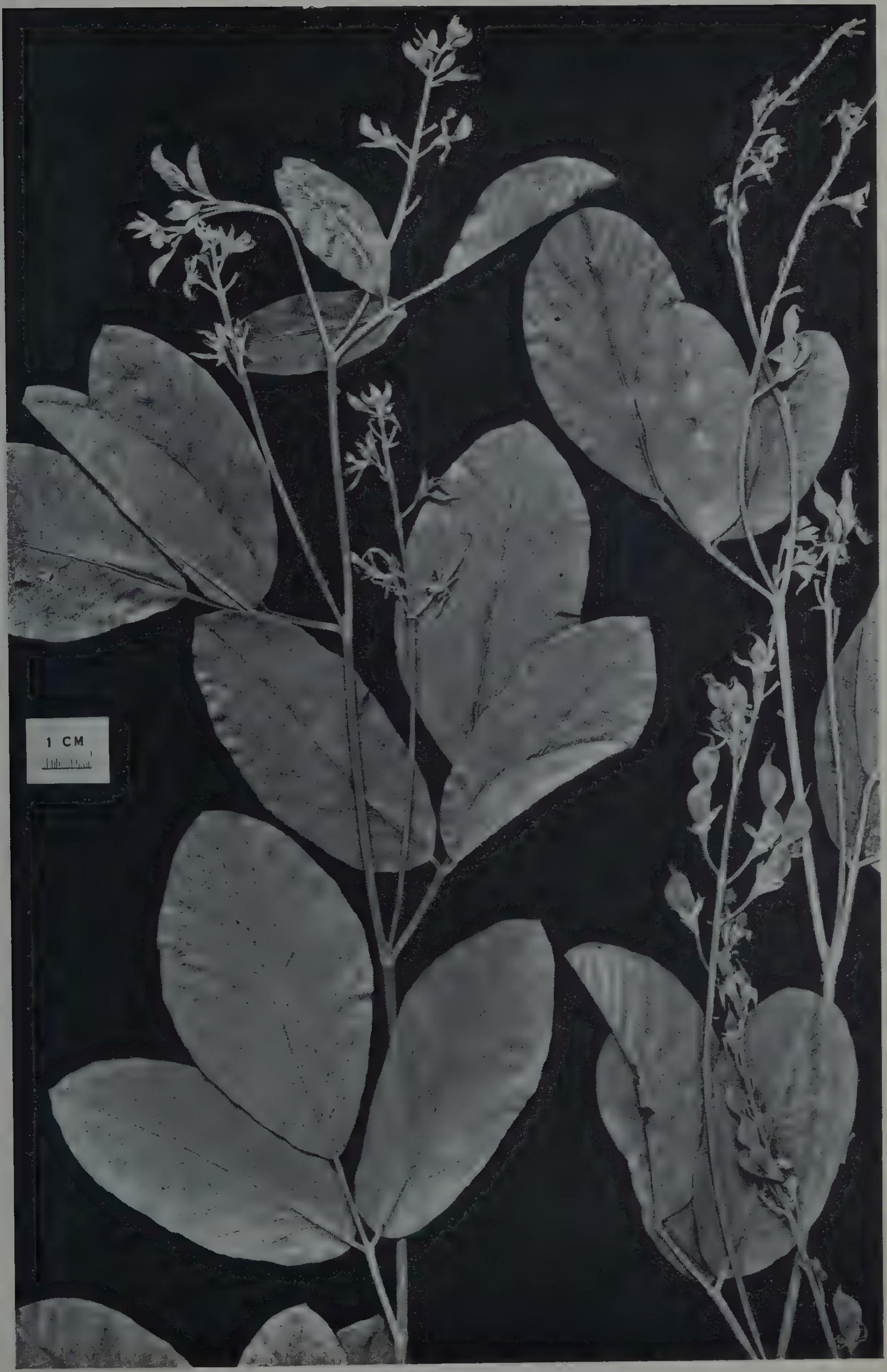
1

2

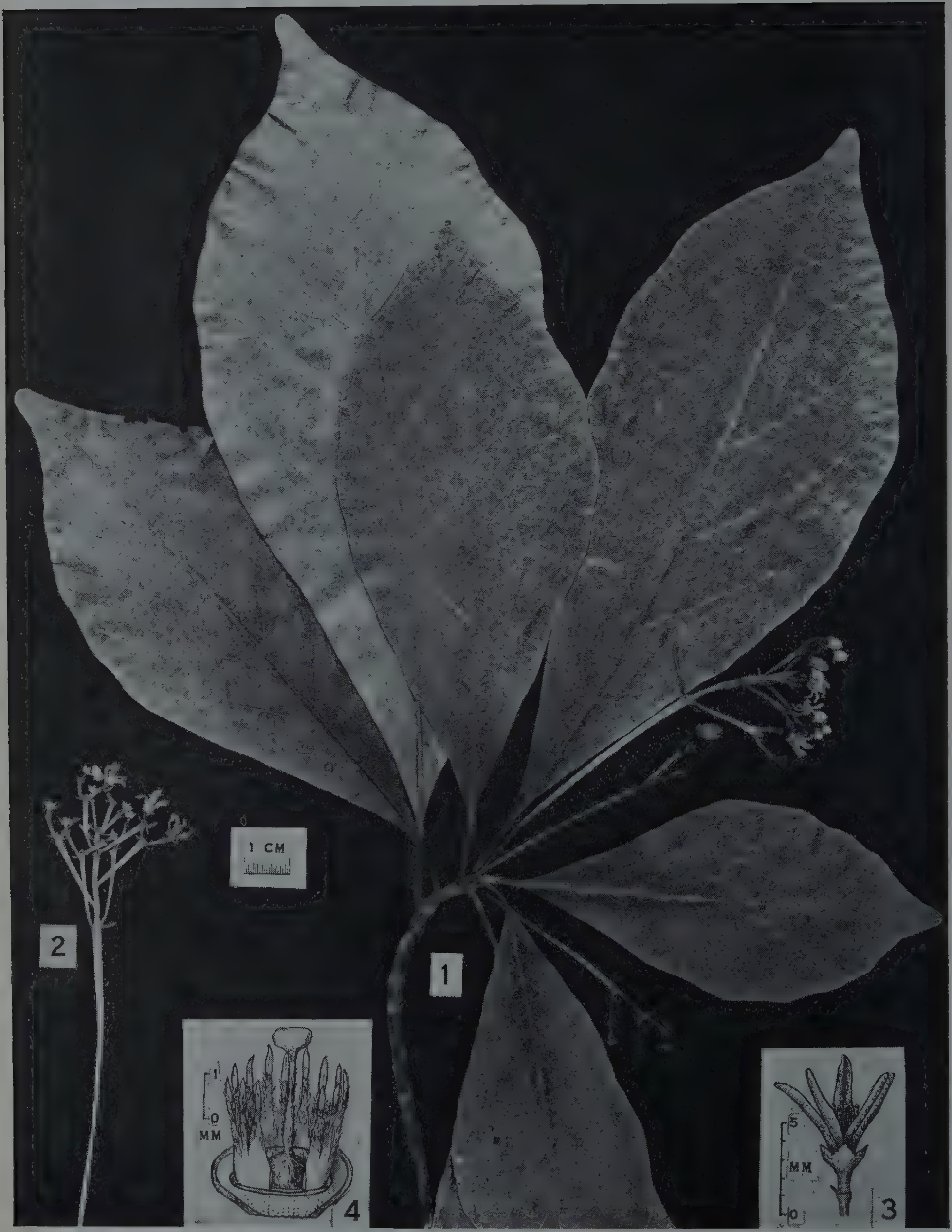
3


4

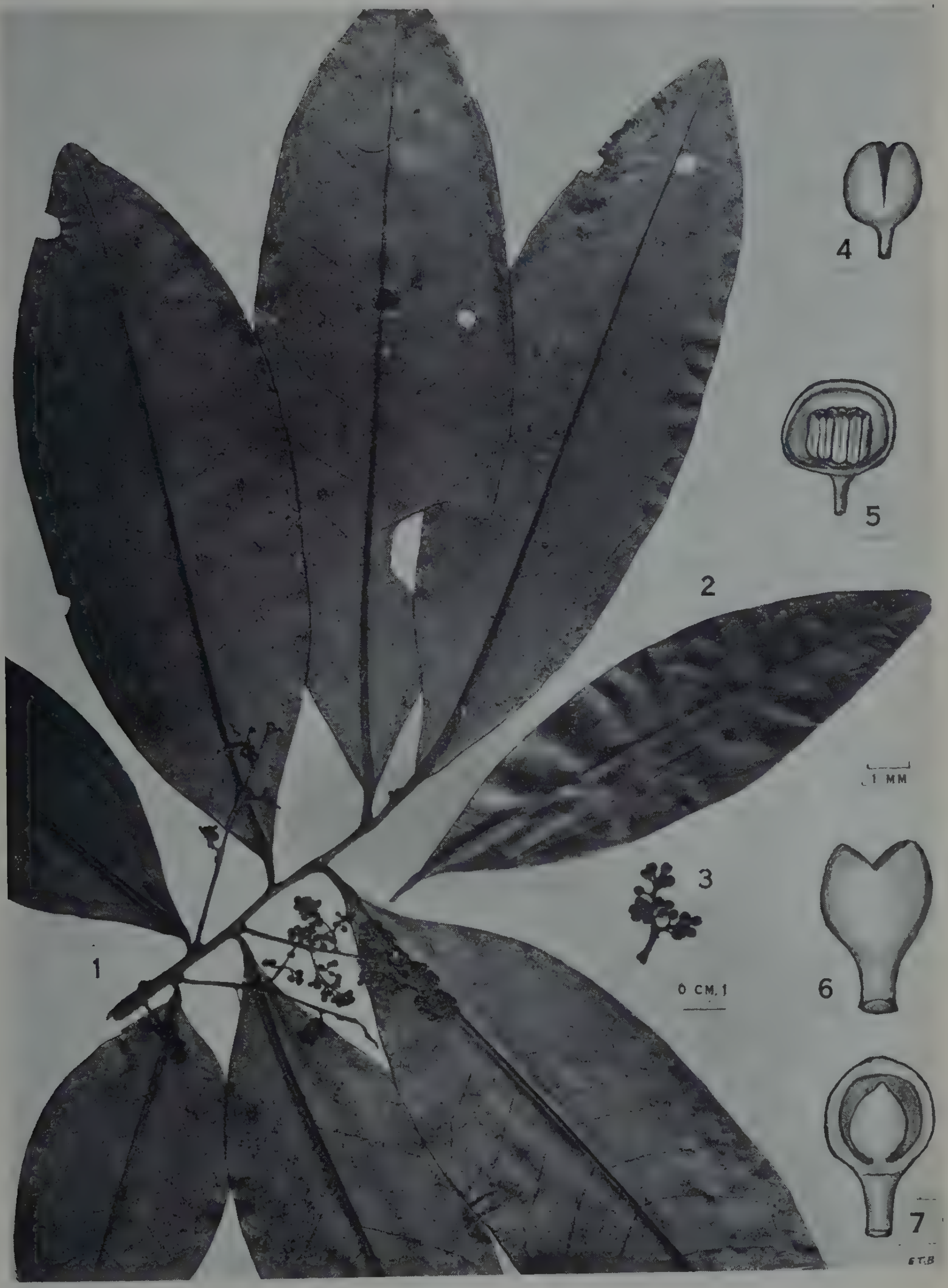

1 CM


1 CM

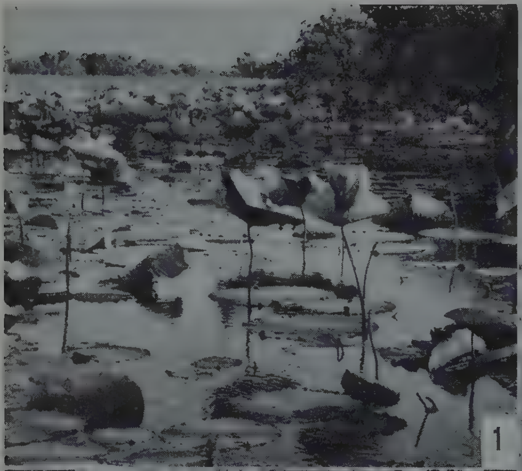
NORTHERN AUSTRALIAN PLANTS


1 CM
1
2
3
4
1
0
MM
5
MM
0

NORTHERN AUSTRALIAN PLANTS


4
5
2
1 MM
3
1
0 CM. 1
6
7
G.T.B

NORTHERN AUSTRALIAN PLANTS


1

2

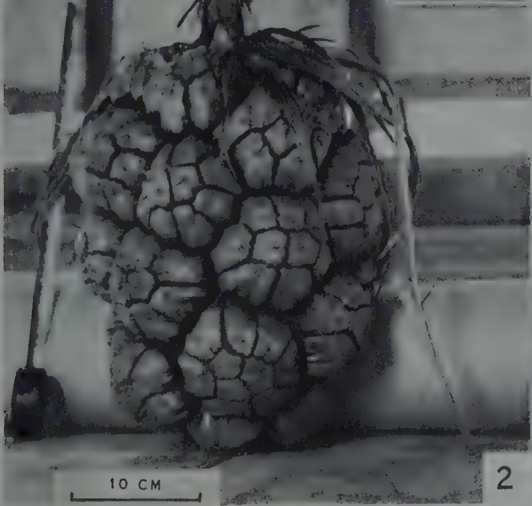
3

4

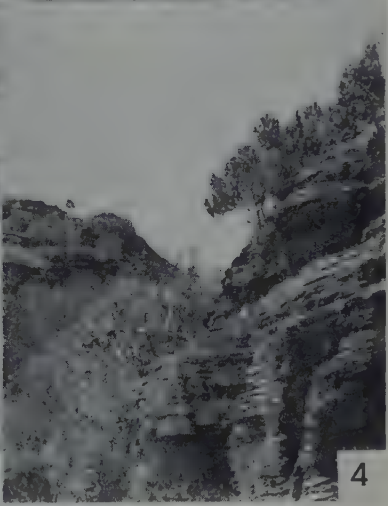
NORTHERN AUSTRALIAN PLANTS

1

3



2


4

INDEX TO NAMES OF FAMILIES AND GENERA

Names of families in capitals and small capitals; accepted names of genera in roman type; synonyms and names mentioned incidentally in italics.

PAGE
Acacia .. 99, 101
Actinophloeus .. 129
Albizia .. 115
Albizzia .. 115
Alectryon .. 135
Alphitonia .. 133
Amorphophallus .. 103
ANACARDIACEAE .. 101
AQUIFOLIACEAE .. 102
ARACEAE .. 103
Atalaya .. 135

Barringtonia .. 104
BARRINGTONIACEAE .. 103
Baryxylum .. 112
Bauhinia .. 113
Bixaceae .. 107
Boronia .. 131
Bruguiera .. 134
Buchanania .. 101
BURSERACEAE .. 106
Byronia .. 102

Caesalpinia .. 112
Campanulaceae .. 137
Canarium .. 106
Carallia .. 134
Carapa .. 121
Cardiospermum .. 135
Careya .. 105
Carpentaria .. 128
Casparia .. 113
Cassia .. 113
Casuarina .. 106
CASUARINACEAE .. 106
Caturus .. 124
Ceanothus .. 133
Ceriops .. 134
COCHLOSPERMACEAE .. 106
Cochlospermum .. 106
Colubrina .. 133
COMBRETACEAE .. 107
Coniogeton .. 102
Corypha .. 128
Cryptocarya .. 111
Cumbia .. 105
Cupania .. 135
Cupaniopsis .. 135

PAGE
CYPERACEAE .. 107
Cyperus .. 107

Dendrolobium .. 117
Desmodium .. 119
Diatoma .. 134
Dichrostachys .. 116
Distichostemon .. 136
Dodonaea .. 136

Erythrophlaeum .. 115
Erythrophleum .. 115
Erythrophloeum .. 115
Eucalyptus .. 100, 101
Eulalia .. 108
EUPHORBIACEAE .. 108

GRAMINEAE .. 108
Gulubia .. 128

Holtzia .. 119
Horsfieldia .. 124
Hydriastele .. 128
Hymenachne .. 108

Ilex .. 102
Inga .. 112, 115

Kentia .. 128

Laboucheria .. 115
LAURACEAE .. 111
Lecythidaceae .. 104
LEGUMINOSAE .. 112
Limonia .. 135
Livistona .. 126

Malaisia .. 124
Maximil(l)ian(e)a .. 106
MELIACEAE .. 121
Micromelum .. 135
Mimosa .. 114
MORACEAE .. 124
Munronia .. 123
Myristica .. 124
MYRISTICACEAE .. 124
Myrtaceae .. 103

Nelumbium .. 126
Nelumbo .. 126

PAGE
Neptunia 116
Nymphaea 126
NYMPHAEACEAE 126
Nurmonia 123

Owenia 121

PALMAE 126
PANDANACEAE 129
Pandanus 129
Panicum 108
Passiflora 132
PASSIFLORACEAE 132
Peltophorum 112
Petalostigma 108
Petalostylis 114
Petalotoma 134
Phanera 113
Phytolacca 137
Piliostigma 113
Pistia 103
Pithecellobium 115
Pithecollobium 115
Pithecolobium 115
PITTOSPORACEAE 132
Pittosporum 132
Planchonia 104, 105
Poinciana 112

PAGE
Pollinia 108
Ptychosperma 128

RHAMNACEAE 133
Rhizophora 133
RHIZOPHORACEAE 133
RUTACEAE 134

SAPINDACEAE 135
Sclerandrium 108
Sonneratia 136
SONNERATIACEAE 136
Sphenoclea 137
SPHENOCLEACEAE 137
Stravadium 104

Terminalia 107
Thouinia 135
Turraea 123

Vavaea 122
Vavea 123

Xylocarpus 121

Ziziphus 133
Zizyphus 133
Zygia 115

THE WOOD ANATOMY OF NEW GUINEA *NOTHOFAGUS* Bl.

By H. E. Dadswell* and H. D. Ingle*

(*Manuscript received January* 15, 1954)

Summary

An examination has been made of the secondary wood of available species of the genus *Nothofagus* Bl. From the results it appears that on the basis of wood anatomy a ready separation can be made into two distinct groups within the genus: one comprising the New Guinea species (eight examined) and the other the temperate species from South America, New Zealand, and eastern Australia (14 examined). The New Guinea species can be separated easily from the remainder by the larger, less numerous vessels, the distinct bands of parenchyma, and the absence of tracheids. The results support the segregation of the New Guinea species into a separate subsection of the genus as proposed by van Steenis (1953).

I. Introduction

Brass (1941), in his account of the Third Archbold Expedition, 1938-39, to the Snow Mountains of Netherlands New Guinea, referred to the extensive *Nothofagus* forests in the mountain regions visited. Reports of similar forests in eastern New Guinea had also been received. The first wood specimens examined by us were collected during 1944 by personnel of the Forest Survey Unit of the Australian Army in eastern New Guinea; these specimens, namely M. R. Jacobs N.G.F. 80 from Edie Creek and L. S. Smith N.G.F. 1098 from Aiyura, were not recognized as *Nothofagus* although placed in the Fagaceae. The late Mr. C. T. White, who was associated with the examination of the early N.G.F. collections, forwarded a sheet of N.G.F. 1098 to the Arnold Arboretum, and in December 1946 was advised of its very great resemblance to some of the Brass collections at that time provisionally assigned to *Nothofagus*. We queried this determination on the basis of wood anatomy because the two New Guinea specimens we had examined did not agree in a number of features with specimens of the genus from Australia, New Zealand, and South America, which anatomically, form a very compact homogeneous unit. The main differences were in the size and number of vessels and in the abundance and distribution of the parenchyma. The New Guinea specimens had the larger vessels (150-190 μ average of maximum tangential diameters as against 50-110 μ), and parenchyma in numerous apotracheal irregularly spaced bands (as against a virtual absence). At this stage therefore we tentatively explored with Mr. White the possibility of a separate genus. However, in May 1947 Mr. White passed on to us some further information from the Arnold Arboretum, including the

---

* Division of Forest Products, C.S.I.R.O., South Melbourne.

following statements by Professor I. W. Bailey: "I have examined the nodes, bark, and wood of the specimens from Dutch New Guinea. Structurally the specimens closely resemble *Nothofagus.* In fact the structure is just about what one would expect in a species of *Nothofagus* from a tropical montane habitat. . . . The pollen of the new plants are typical of *Nothofagus.* . . . It seems to me that a new section of the genus is all that is warranted by the evidence that I have examined . . . "

Further, Langdon (1947) in her examination of the comparative morphology of the genus compared the New Guinea specimens with the various known species and concluded that: "The beeches from Netherlands New Guinea concerning which there has been some question as to position in the Fagacean series have been found to exhibit a combination of morphological characters in their foliage and reproductive structures which is distinctly that of *Nothofagus,* although in certain respects they are sufficiently unlike the more typical members of that genus to justify their reference to a new section of the evergreen beeches."

In the section referred to Langdon also included *N. cliffortioides* Oerst. and *N. solandri* Oerst. from New Zealand.

Additional wood specimens from eastern New Guinea then came to hand and it was of considerable interest to note that all had the same typical anatomical features as the two earlier specimens. In 1950, while Dr. C. G. G. J. van Steenis, to whom the various collections of the New Guinea material had been referred, was in Australia, we discussed the question of the classification of this material, reference being made to the anatomical differences mentioned above. Dr. van Steenis was in no doubt that it should be assigned to *Nothofagus,* although very interested in the anatomical evidence. In 1952 he published a preliminary note on Papuan *Nothofagus* describing 16 species, and later (1953) a more detailed account of the genus which included a proposed classification and key to the various known species. In this classification, a brief outline of which is given in Table 1, there are five subsections, and in subsection 5 all the New Guinea species fall. The two species *N. solandri* and *N. cliffortioides* grouped by Langdon with the New Guinea species are placed by van Steenis in a separate subsection, 4.

Through the courtesy of the Director of the Forest Research Institute, Bogor, Indonesia, we were able to obtain wood specimens corresponding to certain of the Brass and Versteegh collections. These were identical in structure with the other New Guinea specimens already examined. We have therefore undertaken a detailed examination of all available wood specimens of the genus in order to make a comparison between the New Guinea species and the species of the temperate regions.

Other workers have studied the anatomy of the temperate species, e.g. Garratt (1924), Parham (1933), Yatsenko-Khmelevsky (1945), Metcalfe and Chalk (1950), Mouranche (1951), and Paddon (1953).

TABLE 1

SPECIES OF NOTHOFAGUS IN THE SECTIONS AND SUBSECTIONS OF THE GENUS PROPOSED BY VAN STEENIS (1953)

- I. Section Calucechinus (Hombr. & Jacq.) Krasser
  - Subsection 1. Antarcticae Steen.
    - *A.* **N. obliqua* (Mirb.) Oerst.
      - *N. glauca* (Phil.) Krasser
      - *N. alessandri* Espinosa
      - **N. gunnii* (Hook. f.) Oerst.
      - **N. antarctica* (Forst.) Oerst.
    - *B.* *N. alpina* (Poepp. & Endl.) Oerst.
      - **N. procera* (Poepp. & Endl.) Oerst.
  - Subsection 2. Pumiliae Steen.
    - **N. pumilio* (Poepp. & Endl.) Krasser
- II. Section Calusparassus (Hombr. & Jacq.) Krasser
  - Subsection 3. Quadripartitae Steen.
    - *A.* **N. menziesii* (Hook. f.) Oerst.
      - **N. cunninghamii* (Hook. f.) Oerst.
      - **N. moorei* (F. Muell.) Krasser
    - *B.* **N. fusca* (Hook. f.) Oerst.
      - **N. truncata* (Colenso) Cockayne
      - **N. betuloides* (Mirb.) Oerst.
      - *N. nitida* (Phil.) Krasser
      - **N. dombeyi* (Mirb.) Oerst.
  - Subsection 4. Tripartitae Steen.
    - **N. solandri* (Hook. f.) Oerst.
    - **N. cliffortioides* (Hook. f.) Oerst.
  - Subsection 5. Bipartitae Steen.
    - *A.* Series Triflorae Steen.
      - **N. perryi* Steen.
      - *N. recurva* Steen.
      - *N. starkenborghi* Steen.
      - **N. brassi* Steen.
    - *B.* Series Uniflorae Steen.
      - *N. pullei* Steen.
      - *N. crenata* Steen.
      - **N. resinosa* Steen.
      - *N. pseudoresinosa* Steen.
      - **N. carri* Steen.
      - *N. cornuta* Steen.
      - *N. bernhardi* Steen.
      - **N. grandis* Steen.
      - *N. decipiens* Steen.
      - **N. rubra* Steen.
      - **N. eymae* Steen.
      - **N. dura* Steen.

---

* Indicates species of which wood specimens were available for examination.

Mouranche has also compared the anatomy of *Fagus* and *Nothofagus*, and recently Shamaji (1953) has studied in detail the wood of some species of *Fagus*. To complete the present investigation reference has been made to the structure of *Fagus* in comparison with both temperate and New Guinea species of *Nothofagus*.

The distribution of the known species of *Nothofagus* is shown in Figure 1.

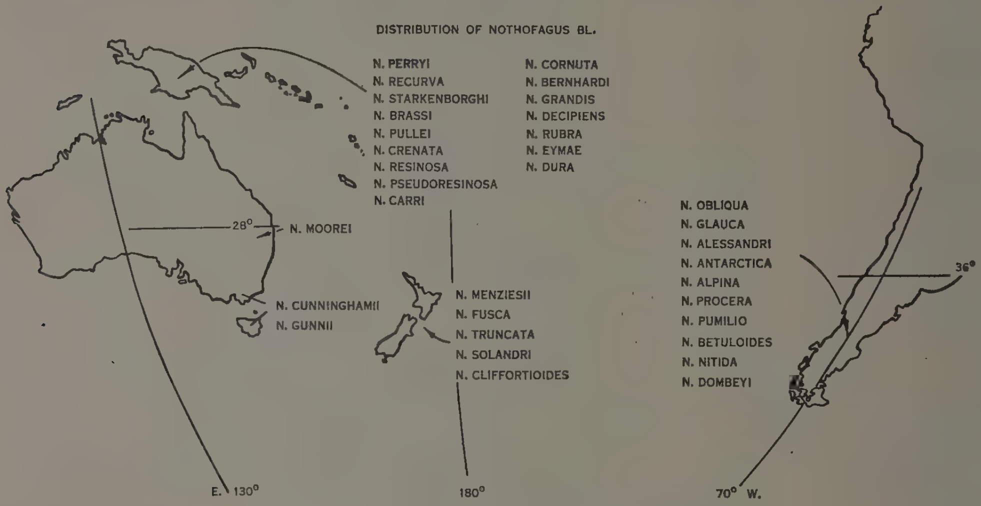

DISTRIBUTION OF NOTHOFAGUS BL.
N. PERRYI
N. RECURVA
N. STARKENBORGHI
N. BRASSI
N. PULLEI
N. CRENATA
N. RESINOSA
N. PSEUDORESINOSA
N. CARRI
N. CORNUTA
N. BERNHARDI
N. GRANDIS
N. DECIPIENS
N. RUBRA
N. EYMAE
N. DURA
28°
N. MOOREI
N. CUNNINGHAMII
N. GUNNII
N. MENZIESII
N. FUSCA
N. TRUNCATA
N. SOLANDRI
N. CLIFFORTIOIDES
N. OBLIQUA
N. GLAUCA
N. ALESSANDRI
N. ANTARCTICA
N. ALPINA
N. PROCERA
N. PUMILIO
N. BETULOIDES
N. NITIDA
N. DOMBEYI
36°
E. 130°
180°
70° W.

Fig. 1.—Distribution of *Nothofagus* Bl.

II. Wood Anatomical Characteristics of Species Examined

Mature wood specimens of eight New Guinea species, six South American, five New Zealand, and three Australian, were examined macroscopically and microscopically. From the results obtained it was immediately apparent that the various species could be segregated into two distinct and compact groups, one comprising all the New Guinea species and the other comprising the remainder. This was not unexpected and supported our earlier contention based on the examination of the original two New Guinea specimens.

For convenience the essential anatomical features of the two groups have been set out in Table 2, in which results of the examination of six species of the genus *Fagus* have also been included. Full anatomical details for each group are given below.

(*a*) Nothofagus *A**

(i) *General*.—These species occur in the south temperate regions of Argentine, Chile, New Zealand, Tasmania, and eastern Australia at elevations up to about 6000 ft, generally south of latitude 36°, except

---

* Covering species listed by van Steenis in his subsections 1-4 inclusive.

TABLE 2

ANATOMICAL DIFFERENCES BETWEEN NEW GUINEA AND TEMPERATE NOTHOFAGUS; FEATURES OF FAGUS ALSO LISTED FOR COMPARISON

Feature	*Nothofagus* Bl.		*Fagus* (Tourn.) L.
	Subsections 1-4 Steen. (temperate)	Subsection 5 Steen. (New Guinea)	
Vessels			
Number/sq. mm.	60-100+	9-16	70-100
Av. max. tangential dia.	50-100 μ	125-190 μ	72-90 μ
Av. member length	420-880 μ	720-950 μ	360-660 μ
Solitary (%)	20-50	36-58	90
Pitting	Opposite to sometimes scalariform	Alternate to opposite, occasionally scalariform	Alternate, or loosely arranged with some opposite tendency
Pit size, shortest border dia.	6-7 μ	7-10 μ	6-8 μ
Perforation plates	Simple, sometimes transitional to scalariform in small late wood vessels	Simple	Simple, to simple and scalariform with 6-10 bars
Rays			
Width	1-2 (3) Cells	1-2 (3) Cells	(*a*) 1-5 and (*b*) 14-25
Type	Heterogeneous, 1-2 rows square to upright cells	Heterogeneous, 1-6 rows square to upright cells	Practically homogeneous
Siliceous inclusions	Present in *N. solandri*, *N. cliffortioides*, and *N. truncata* (to a lesser extent)	Absent	Absent
Parenchyma			
Arrangement	Apotracheal, sparse, usually scattered cells at end of growth zone	Apotracheal, in fairly numerous irregularly spaced bands 2-6 cells wide, a little diffuse	Apotracheal, diffuse to reticulate, more abundant in late wood
Crystal strands	Occasionally present	Present, large crystals sometimes moderately abundant	Absent
Fibres			
Septa	Sporadic in most species	Sparse to absent	Absent
Pitting	Simple	Simple	Distinctly bordered
Av. length	0.70-1.16 mm	1.20-1.48 mm	0.96-1.48 mm
Tracheids	Present	Absent	Absent

N. moorei, which is found in eastern Australia as far north as latitude 28°. They are chiefly large trees but sometimes forming prostrate shrubs (e.g. *N. antarctica* and *N. gunnii*) at upper elevations; sometimes in pure stands or mixed with conifers or broad-leaved rain-forest species. Heartwood is generally pale pink to dark red or red-brown in colour, sapwood white to very pale brown, often wide and grading into a zone of intermediate wood; in general moderately light to moderately heavy, up to 49 lb/cu. ft. air dry; texture very fine and uniform, with slight figure on backsawn surfaces due to distinct growth rings; generally straight-grained and moderately fissile. Many species are of commercial importance and are known on the world's timber markets.

(ii) *Structure.—Growth rings* generally well marked in all species (but to a lesser extent in *N. moorei*) by a band of thicker-walled fibres and smaller vessels distinguishing the last-formed late wood and in some samples by a ring of larger pores in the first-formed early wood (see Plate 2, Figs. 1 and 3; Plate 3, Figs. 1-4). *Vessels* small to very small, indistinct to invisible to the naked eye; average maximum tangential diameters varying from 50 to 110 μ in different species; average member length 420-880 μ; evenly distributed, but frequently grading in size from early to late wood; very numerous, 60-100+/sq. mm.; solitary and in radial multiples of 2-5 cells, but occasionally up to 8 or more as in *N. cliffortioides;* some clusters present; in cross section somewhat angular in shape when solitary; pitting opposite, or with a strong opposite tendency, to sometimes scalariform; pits medium-sized, with shortest diameter 6-7 μ; perforation plates predominantly to exclusively simple except in smallest pores at the end of the late wood where some plates transitional to scalariform may be observed; spirals present and of regular occurrence in *N. moorei, N. obliqua,* and *N. pumilio,* sporadic in tips of elements in *N. procera;* tyloses present in all species. *Rays* 1-2-seriate (Plate 2, Fig. 5), occasionally triseriate; uniseriate varying from few to many in some species, of same type as multiseriate; weakly heterogeneous with 1-2 rows of square to sometimes upright cells; maximum height up to 30 cells; vessel-ray pitting half-bordered, with wide aperture and narrow border, appearing simple, rounded to horizontally elongated with a tendency to scalariform arrangement (Plate 2, Fig. 4), confined to marginal square and upright cells; crystals absent; siliceous inclusions in 3 species, *N. solandri, N. cliffortioides,* and to a lesser extent in *N. truncata,* sometimes concentrated in late wood zone of the growth ring; deposits of extraneous material sometimes common. *Parenchyma* apotracheal, sparsely diffuse in the late wood, or more often at junction of early and late wood; occasionally forming an almost complete tangential line in *N. moorei* (Plate 2, Fig. 2); crystal strands occasionally present, sometimes comparatively common. *Fibres* with wall thickness generally less than diameter of lumen except in late wood; sporadically septate in all species, although generally non-septate; pits small, simple, and moderately numerous; mean length varying from 0.70 to 1.16 mm. *Tracheids* confined to last few rows of late wood, present in majority of species.

(iii) *Material.—N. antarctica* (Forst.) Oerst. (2 samples, Chile, Argentine); *N. betuloides* (Mirb.) Oerst. (2, Argentine); *N. cliffortioides* (Hook. f.) Oerst. (2, New Zealand); *N. cunninghamii* (Hook. f.) Oerst. (8, Tasmania and Victoria); *N. dombeyi* (Mirb.) Oerst. (4, Chile and Argentine); *N. fusca* (Hook. f.) Oerst. (4, New Zealand); *N. gunnii* (Hook. f.) Oerst. (2, Tasmania); *N. menziesii* (Hook. f.) Oerst. (3, New Zealand); *N. moorei* (F. Muell.) Krasser (5, New South Wales and south-eastern Queensland); *N. obliqua* (Mirb.) Oerst. (2, Argentine and Chile); *N. procera* (Poepp. & Endl.) Oerst. (5, Argentine and Chile); *N. pumilio* (Poepp. & Endl.) Krasser (3, Argentine and Chile); *N. solandri* (Hook. f.) Oerst. (1, New Zealand); *N. truncata* (Colenso) Cockayne (1, New Zealand).

(*b*) Nothofagus *B**

(i) *General.*—These species occur in the mountainous areas of east and west central New Guinea, from 2700 ft (*N. grandis*) up to 9000 ft; mostly dominant or co-dominant trees in the fagaceous montane rain-forests often associated with *Podocarpus* and *Libocedrus* (Mt. Hagen area), and *Weinmannia* and *Metrosideros* in west central New Guinea; large trees up to 120 ft high, narrowly buttressed at the base (Mt. Hagen and Aiyura); heartwood golden-brown to red-brown in colour, sapwood pale brown, $1\frac{1}{2}$ in. wide but grading into an intermediate zone; moderately heavy to heavy; texture uniform and moderately fine.

(ii) *Structure* (Plate 1, Figs. 1-4).—*Growth rings* not evident. *Vessels* indistinct to visible to the naked eye; average maximum tangential diameters varying from 125 to 190 μ; average member length 720-950 μ; moderately numerous to numerous, 9-16/sq. mm.; evenly distributed, 36-60 per cent. solitary (tending to be elongated radially in cross section), in radial multiples commonly 2-4, sometimes up to 6, clusters present; perforation plates simple, horizontal to oblique; inter-vessel pitting bordered, moderately coarse, alternate to opposite with occasionally a scalariform tendency, shortest diameters of borders 7-10 μ; tyloses abundant; spiral thickenings observed in tips of elements, sporadically to consistently present in *N. brassi, N. carri, N. grandis,* and an indeterminate sample from eastern New Guinea. *Rays* predominantly 1-2-seriate, occasionally triseriate; uniseriate sometimes up to 40 per cent.; weakly to definitely heterogeneous, the marginal cells varying from a few square to sometimes 5 rows of upright, uniseriate often of square to upright cells; maximum height up to 30 cells; vessel-ray pitting coarse, half-bordered with large aperture and narrow border often appearing simple; rounded to irregular and elongated, often in scalariform arrangement, not always confined to marginal cells, siliceous inclusions and crystals wanting; deposits of extraneous material moderately abundant. *Parenchyma* apotracheal, mainly in irregularly spaced bands, 2-6, occasionally up to 9 cells wide, sometimes discontinuous, frequently appearing sinuous or crenate in transverse section; diffuse often present but never abundant and may be sparse to absent; crystal strands present, individual cells sometimes enlarged and each containing a large crystal. *Fibres* moderately thick-walled, with lumen diameter smaller than wall thickness; occasionally septate; pits simple; mean length varying from 1.20 to 1.48 mm. *Tracheids* absent.

---

* Covering species listed by van Steenis in his subsection 5.

(iii) *Material.*—*N. brassi* Steen., Brass and Versteegh, 11,103 and 11,115; *N. carri* Steen., N.G.F. 3328 and N.G.F. 3330; *N. dura* Steen., Brass and Versteegh 10,443; *N. eymae* Steen., Brass and Versteegh 11,963; *N. grandis* Steen., Brass and Versteegh 12,553, N.G.F. 1098, N.G.F. 3320, N.G.F. 3389, N.G.F. 5366; *N. perryi* Steen., N.G.F. 5356; *N. resinosa* Steen., Brass and Versteegh 10,448 and 10,479; *N. rubra* Steen., Brass and Versteegh 11,997; *N.* sp. indt. N.G.F. 3323.

III. DISCUSSION

It is particularly interesting to note from the examinations carried out that there is such a distinct segregation into two distinct populations, namely tropical and temperate species, on the basis of wood anatomy, and further that there is no evidence of any species showing what might be termed intermediate features (with the possible exception of *N. moorei*).

Van Steenis was able to make a definite division in the New Guinea subsection on the basis of floral characteristics, but species of both the series Triflorae and Uniflorae were essentially identical in wood structure. The temperate species fell into four subsections botanically but, on the basis of wood anatomy, no essential differences were observed with perhaps the exception that *N. solandri* and *N. cliffortioides* of subsection 4 showed distinct accumulation of silica.

Admittedly the feaures of difference between tropical and temperate groups, which are shown clearly in Table 2 and in the photomicrographs, are not fundamental in character. Both have fibres with simple pits, generally similar types of vessel and ray-vessel pitting, absence or virtual absence of multiple perforation plates, heterogeneous rays of similar size, and some septate fibres (although these are of more frequent occurrence in the temperate species). The New Guinea species are characterized by larger, less numerous vessels, numerous irregularly spaced bands of parenchyma 2+ cells wide, prominent crystals in the parenchyma cells, and the absence of tracheids. The parenchyma bands and the larger vessels are very distinct macroscopically and, on the basis of hand lens examination of the wood, immediately separate the New Guinea material from all the temperate species of the genus. It was this combination of features that led to our original query regarding the identification of the New Guinea woods as *Nothofagus*.

All the temperate species examined have more or less distinct growth rings with very numerous small vessels diminishing somewhat in size through the growth ring and with practically no parenchyma observable under the hand lens. Microscopic examination shows that scattered parenchyma cells do occur in this group towards the end of the growth ring, and in some samples of *N. moorei* there is a tendency to form a concentric terminal or initial band of parenchyma. This species of the temperate group is the one found furthest north in the southern hemisphere.

In the New Guinea material the irregularly spaced bands of parenchyma already referred to may perhaps indicate growth zones, but there is no definite evidence that this is so. In other features there are slight divergences between the two groups; for example, the vessel and ray-vessel pitting are not absolutely identical, although there is some overlapping. The rays of the New Guinea material show a greater tendency to heterogeneity with more marginal rows of square to upright cells.

The evidence from the anatomy of the wood supports the botanical grouping of the New Guinea material into a distinct subsection as proposed by van Steenis (1953). There is no support for the grouping of this material with *N. solandri* and *N. cliffortioides* as suggested by Langdon (1947). After due consideration we believe that the anatomical differences between the New Guinea and temperate species cannot demand more than a separate section within the genus, especially as other features are characteristic of the genus as a whole. Wood anatomy on its own cannot determine taxonomy; however, when wood anatomical evidence supports other evidence, some consideration should be given to it. In the present instance there appears no doubt botanically as to the correct placing of the New Guinea material.

There are numerous examples in wood anatomy where some members of a genus have anatomical features distinct from other members of the same genus. One such example is *Eucalyptus*, which we have already indicated (Ingle and Dadswell 1953) can be split into two distinct groups. Again, *Eugenia* (sens. lat.) has been subdivided into two main groups on anatomical grounds (Ingle and Dadswell 1953), but here there is considerable botanical evidence that two or more genera are involved.

In such features as the regular occurrence of almost homogeneous wide rays, the presence of fibre tracheids, the predominance of solitary vessels, and the diffuse to reticulate parenchyma, the species of the genus *Fagus* are immediately separable from those of *Nothofagus*. It is of interest to note, however, that apparently normal rays six to eight cells wide were observed in *N. betuloides* and *N. dombeyi* of the temperate species and in *N. grandis* from New Guinea. Paddon (1953) also has recorded the occasional presence of rays five cells wide in *N. antarctica*. It may be that the observed differences indicate diverging lines of specialization rather than lack of affinity.

The two groups of *Nothofagus* themselves show diverging lines of specialization, and it is interesting to note that the temperate species have the shorter fibrous and vascular elements, which may be considered a more advanced character. On the other hand the predominance of opposite to scalariform pitting in the temperate species as compared with the New Guinea species is a relic of more primitive characters.

Parham (1933) has referred to the presence of pitted tracheids and transitional elements occurring sparingly in the temperate species of *Nothofagus*. In the present examination, elements with numerous distinctly bordered pits were observed at the end of the growth ring in many of the temperate species. It was thought at first that these were imperfect vessel elements, and they were often found consistently in the last two or three files of cells in any growth ring. The last-formed wood of a growth ring in *N. pumilio* (a species consistently showing spiral thickening of the vessel elements) was macerated. Imperfect vessel elements with spiral thickening and transitional to scalariform perforation plates were observed but, in addition, other cells of similar dimensions but lacking either perforation plates or spiral thickenings, were common. The bordered pits in these cells were not as coarse as those in the vessel elements. Cells of this type have been referred to as tracheids in this paper. It was also noted that where these elements were adjacent to vessels in the early wood, intercommunicating pits were present, whereas in the rest of the growth ring there was no communication between the libriform fibres and adjacent vessels. These tracheids are absent from the New Guinea species. It is possible that they perform part of the function carried out by the concentric bands of parenchyma present in the woods of the New Guinea group, especially as they are not so characteristic of *N. moorei*, which has relatively more abundant initial parenchyma and less marked growth rings than most of the others of the temperate group.

Van Steenis (1953) has mentioned the five species of Fagaceae collected in New Caledonia by Dr. M. G. Baumann-Bodenheim of Zürich; these species have been referred to the genus *Trisyngyne* (Baumann-Bodenheim 1953). Dr. Baumann very kindly forwarded to us, for the examination of wood structure, twig specimens from his herbarium material. These specimens were sectioned and examined microscopically.

The wood structure was compared with that from twigs of *Nothofagus carri* and *N. grandis* from New Guinea, and from *N. solandri, N. cunninghamii, N. menziesii,* and *N. moorei* of the temperate group. Although definite conclusions cannot be drawn on the basis of twig material only, it was of interest to us to note that Dr. Baumann's material was anatomically similar to the New Guinea species, although not identical with them, and quite distinct from the twig material of the temperate species. Dr. Baumann's New Caledonian species showed abundance of parenchyma in the first-formed secondary wood, this parenchyma being in distinct concentric bands several cells wide. In the New Guinea material the concentric parenchyma bands of the mature wood were not nearly so definite in the young twigs, although these twigs in other respects were identical anatomically with the mature wood. We are looking forward to obtaining for examination mature wood specimens of these new Caledonian species.

In conclusion it may be said that the wood anatomical evidence is not inconsistent with the theory proposed by van Steenis, namely that the New Guinea species of *Nothofagus* are living relics of a former more widely distributed genus, the temperate group being derivative from this. Further support of this is derived from the examination of pollen type. Cookson (1952) has found close agreement between the pollen of living New Guinea *Nothofagus* and a type of fossil pollen from Tertiary beds in eastern Australia. This pollen type occurs from Queensland to Tasmania and into South Australia, but does not match the two other pollen types found in the living temperate species of *Nothofagus.* As yet, to our knowledge, no fossilized wood specimens from eastern Australia showing the anatomical structure of either the New Guinea *Nothofagus* or the temperate *Nothofagus* have been found.

IV. ACKNOWLEDGMENTS

The authors express their thanks to Dr. C. G. G. J. van Steenis for his kindness and cooperation in making available the manuscript of his paper on Papuan *Nothofagus,* and for his assistance in obtaining wood samples corresponding to the Brass collection made in Netherlands New Guinea; to the Director, Forest Research Institute, Bogor, Indonesia, for supplying the above wood samples; to Dr. M. G. Baumann-Bodenheim for sending us small twig specimens cut from the Fagaceae material he collected in New Caledonia; to the Director, Mr. J. B. McAdam, and the Forest Botanist, Mr. J. S. Womersley, of the Department of Forests, Territory of New Guinea, for supplying wood samples of various species of *Nothofagus* collected in eastern New Guinea; and finally to Miss Margaret Marfleet for assistance in the preparation and preliminary examination of the material.

V. References

BAUMANN-BODENHEIM, M. G. (1953).—Résultats scientifiques de la mission Franco-Suisse de Botanique en Nouvelle-Calédonie. Fagacées de la Nouvelle-Calédonie. *Bull. Mus. Hist. Nat.* (2) 25: 419-21.

BRASS, L. J. (1941).—1938-39 Expedition to the Snow Mountains, Netherlands New Guinea. *J. Arnold Arbor.* 22: 271-342.

COOKSON, ISABEL C. (1952).—Identification of Tertiary pollen grains with those of New Guinea and New Caledonian beeches. *Nature* 170: 127.

GARRATT, G. A. (1924).—Some New Zealand woods. Prof. Pap. N.Z. St. For. Serv. No. 1.

INGLE, H. D., and DADSWELL, H. E. (1953).—The anatomy of the timbers of the south-west Pacific area. III. Myrtaceae. *Aust. J. Bot.* 1 (3): 353-401.

LANGDON, L. MARY (1947).—The comparative morphology of the Fagaceae. I. The genus *Nothofagus*. *Bot. Gaz.* 108: 350-71.

METCALFE, C. R., and CHALK, L. (1950).—"Anatomy of the Dicotyledons." (Clarendon Press: Oxford.)

MOURANCHE, R. (1951).—Note sur les bois de *Fagus* et de *Nothofagus*. *Rev. Int. Bot. Appl.* 31: 84-90.

PADDON, T. W. (1953).—Les nouveaux hetres de Chile. *Rev. Bois* 8 (5).

PARHAM, B. E. (1933).—New Zealand beech timbers; their structure and identification. *N.Z. J. Sci. Tech.* 14: 233-40, 372-82.

SHAMAJI, K. (1953).—Anatomical studies on the wood of some *Fagus* species. Bull. Tokyo Univ., For. No. 42.

VAN STEENIS, C. G. G. J. (1952).—Preliminary account of Papuan *Nothofagus*. *Blumea* 7: 146.

VAN STEENIS, C. G. G. J. (1953).—Results of the Archbold Expeditions; Papuan *Nothofagus*. *J. Arnold Arbor.* 34: 301-74.

YATSENKO-KHMELEVSKY, A. (1945).—The wood structure of some species of the genus *Nothofagus* in connection with its systematic position. *C.R. Acad. Sci. U.R.S.S.* 2: 109-13.

Explanation of Plates 1-3

Plate 1

Fig. 1.—*Nothofagus grandis* Steen. NGF. 1098. Transverse section showing characteristic pore arrangement and abundance of tyloses; parenchyma typically apotracheal in irregularly spaced bands. × 25.

Fig. 2.—*Nothofagus grandis* Steen. NGF. 1098. Tangential section showing typical biseriate heterogeneous rays and inter-vessel pitting with a tendency to opposite arrangement. × 90.

Fig. 3.—*Nothofagus carri* Steen. NGF. 3330. Tangential section showing diffusely arranged crystal strands. × 90.

Fig. 4.—*Nothofagus grandis* Steen. NGF. 1098. Radial section showing uniseriate ray with characteristic vessel-ray pitting. × 320.

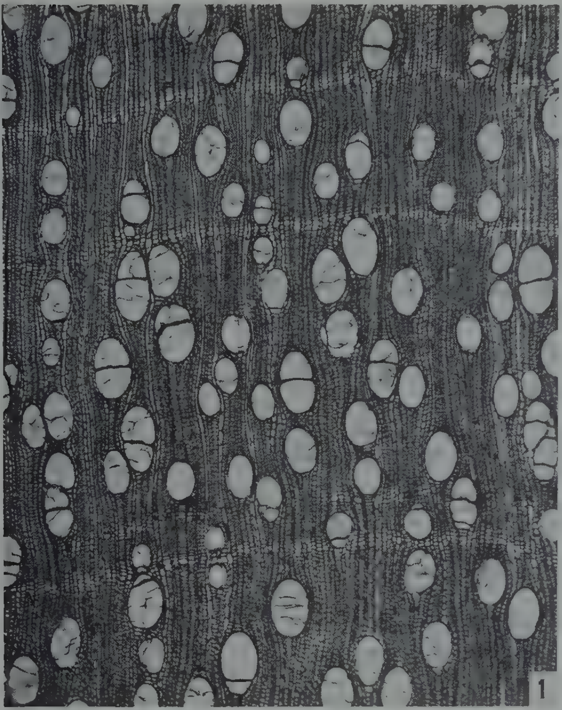
Plate 2

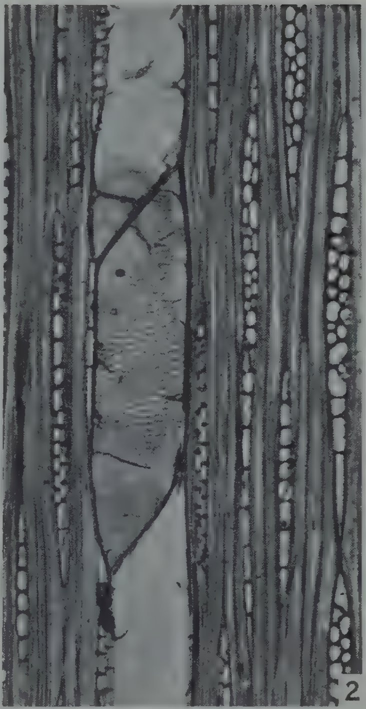
Fig. 1.—*Nothofagus solandri* (Hook. f.) Oerst. Transverse section showing small pores characteristically in multiples (60 μ maximum tangential diameter). × 22.

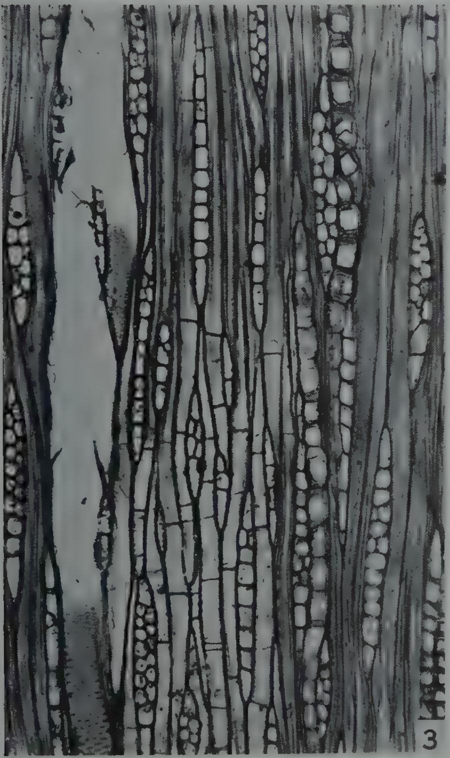
Fig. 2.—*Nothofagus moorei* (F. Muell.) Krasser. Transverse section showing sparse parenchyma at commencement of growth ring. × 155.

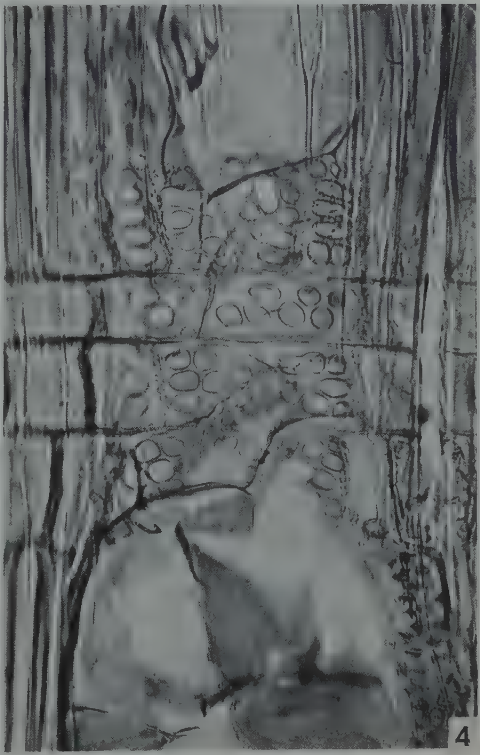
Fig. 3.—*Nothofagus cliffortioides* (Hook. f.) Oerst. Transverse section showing marked growth ring and small pores (50 μ maximum tangential diameter). × 22.

WOOD ANATOMY OF NEW GUINEA NOTHOFAGUS

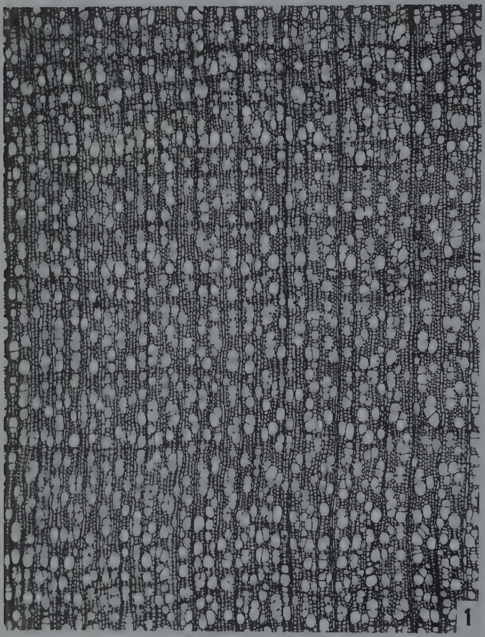

1

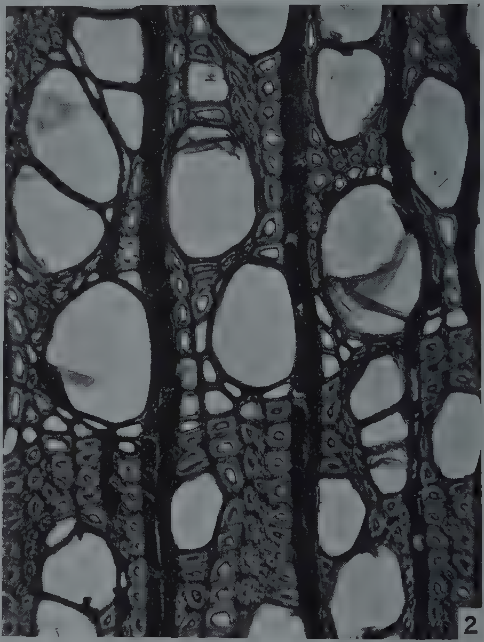

2

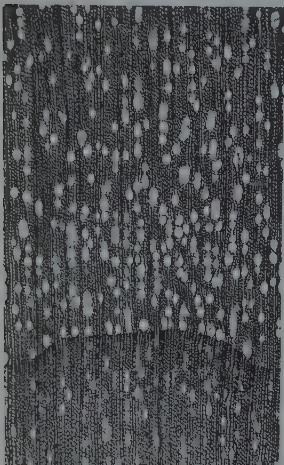

3

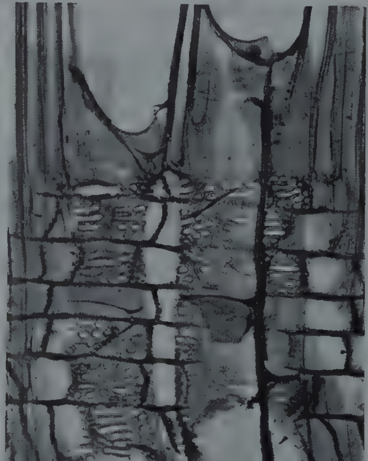

4

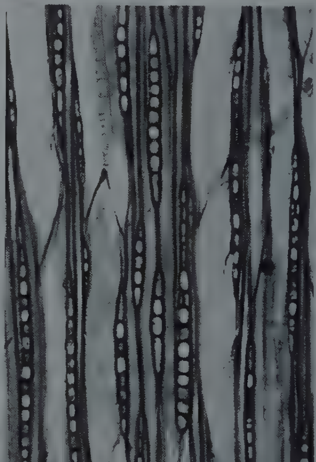
WOOD ANATOMY OF NEW GUINEA NOTHOFAGUS


1

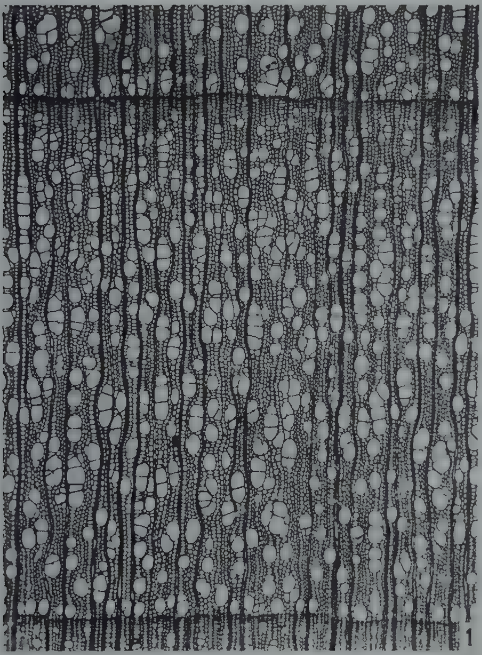

2

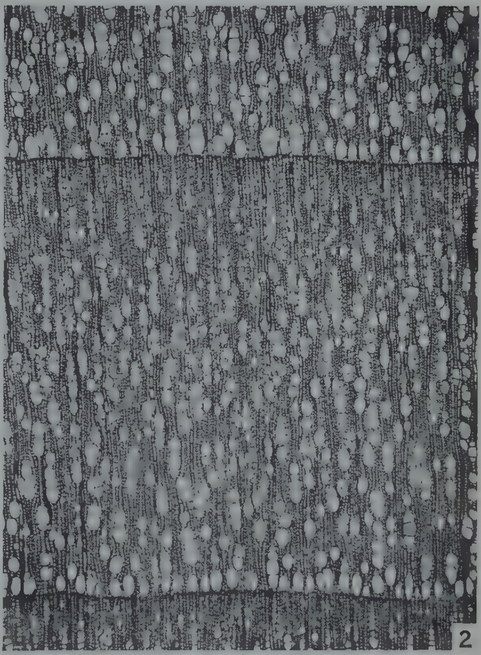

3

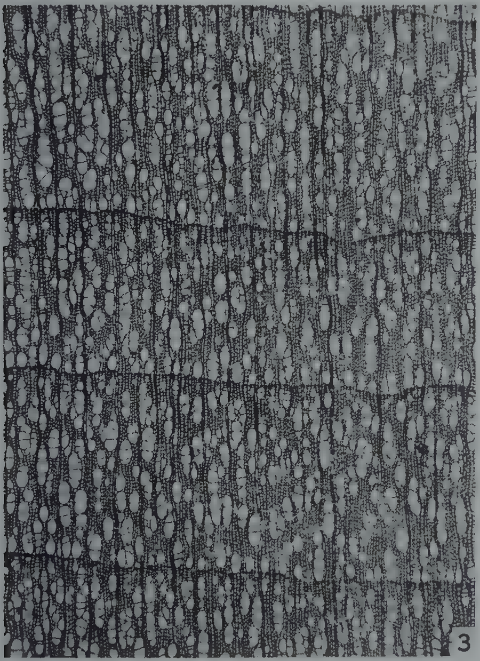

4


5

WOOD ANATOMY OF NEW GUINEA NOTHOFAGUS


1


2


3

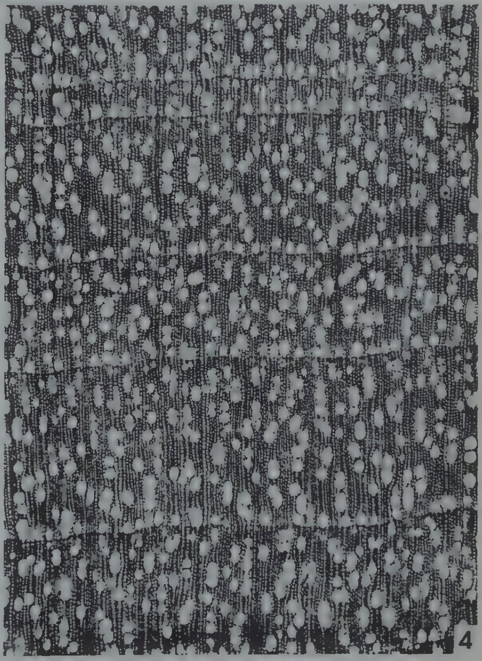

4

Fig. 4.—*Nothofagus fusca* (Hook. f.) Oerst. Radial section showing characteristic vessel-ray pitting confined to marginal rows of cells in the ray. × 155.

Fig. 5.—*Nothofagus solandri* (Hook. f.) Oerst. Tangential section showing high percentage of uniseriate rays and vessel pitting typically opposite to occasionally scalariform. × 80.

PLATE 3

Fig. 1.—*Nothofagus antarctica* (Forst.) Oerst. Transverse section showing pore size and arrangement. × 22.

Fig. 2.—*Nothofagus betuloides* (Mirb.) Oerst. Transverse section showing pore distribution and tendency to ring-porous arrangement. × 22.

Fig. 3.—*Nothofagus dombeyi* (Mirb.) Oerst. Transverse section showing tendency for long radial multiples of pores. × 22.

Fig. 4.—*Nothofagus cunninghamii* (Hook. f.) Oerst. Transverse section showing pore size and distribution. × 22.

OBSERVATIONS ON CROSSED LAMELLAR STRUCTURES IN THE CELL WALLS OF HIGHER PLANTS

By A. B. Wardrop*

(*Manuscript received December* 1, 1953)

Summary

Crossed lamellar structures in cell walls have been known to occur with certainty only in some green algae. A number of higher plants in which it was considered this structure might be present have been examined, and it has been demonstrated in the phloem fibres of *Vinca major* and the tracheidal elements of the aerial root of *Alstonia spathulata*. In the latter two types of crossed structure are recognized, in one bands of laterally associated microfibrils *c.* 0.5 μ wide intersect at variable angles, whereas in the other lateral association is complete, forming a crossed lamellar structure which approaches most nearly that occurring in the algae. In the outer layer of the secondary wall of wood fibres of *Eucalyptus elaeophora* and *E. regnans* there is inconclusive evidence of a crossed structure similar to that observed in the cell walls of some vessels, which consists of a loosely formed meshwork of aggregates of microfibrils. This structure is considered to be distinct from the crossed lamellar and cross-banded structures.

I. Introduction

Crossed lamellar structures have long been known to exist in the cell walls of green algae such as *Valonia* (van Iterson 1933; Preston and Astbury 1937), *Chaetomorpha* (Nicolai and Frey-Wyssling 1938), and *Cladophora* (Astbury and Preston 1940).

In higher plants there is little evidence for the presence of this structure except perhaps in the walls of phloem fibres of *Vinca* (see Strasburger 1930) and in the pith parenchyma of *Dahlia* (Sachs 1882; Strasburger 1924).

It was of some interest therefore that in an electron-microscopic study of the cell walls of conifer tracheids some indication of the presence of this type of structure in the outer or inner layer of the secondary wall was obtained (Hodge and Wardrop 1950). However, on the evidence available it was not possible to decide if the structure observed should be interpreted as arising from the superposition of part of either the outer or inner layer over part of the central layer of the secondary wall, or as meaning that either the outer or inner layer of the secondary wall of tracheids possessed an intrinsic crossed fibrillar structure. Bosshard (1952), from the examination of fibres of *Fraxinus,* suggested that all layers of the secondary wall possessed a crossed fibrillar structure.

In view of the academic interest relating to the possible widespread occurrence of this structure in higher plants and of its technological

---

* Division of Forest Products, C.S.I.R.O., South Melbourne.

implications, as in the beating and swelling of wood fibres, the investigations reported here were undertaken.

II. Methods and Results

Three types of material were examined:

(*a*) Specimens in which crossed fibrillar structures had previously been reported in the literature.

Vinca major.—Phloem fibres. The fibres were separated mechanically, delignified by the holocellulose method, using chlorine water and monoethanolamine, and disintegrated in a Waring Blendor prior to electron-microscopic examination (Plate 2, Fig. 1).

Dahlia sp.—Pith parenchyma from a root tuber. Portions of the pith were macerated with hydrogen peroxide and acetic acid. In a second treatment sections (10 μ) of the pith were cut thinner than the parenchyma cells and then macerated prior to electron-microscopic examination (Plates 3 and 4).

(*b*) Thin-walled vascular tissue which it was considered might resemble in its wall structure the outer layer of the secondary wall in thick-walled tracheids and fibres.

Alstonia spathulata Bl.—Examination of the woody tissue of an aerial root revealed thin-walled vascular elements which appear to be tracheidal in nature (Plate 1, Fig. 1), and in transverse section resemble the parenchyma of *Ochroma* (see below). This material was prepared as with *Dahlia* to give both whole cells and single walls for electron-microscopic examination (Plates 5, 6, and Plate 2, Fig. 2).

Ochroma lagopus Swartz.—In low density specimens of this wood the parenchyma is birefringent in transverse section and shows no layering. Longitudinal sections were cut and macerated as with *Dahlia* to obtain fragments of single cell walls. These were mounted directly for electron-microscopic examination (Plate 7).

(*c*) Partly differentiated xylem was collected from stems of *Eucalyptus elaeophora* F. Muell., *E. regnans* F. Muell., and *Ulmus* sp. early in spring in the manner described by Priestley, Scott, and Malins (1933). In this tissue only the primary wall and occasionally the outer layer of the secondary wall was present.

After optical examination the specimens, suspended in water, were placed on collodion-covered grids, uranium-shadowed at an angle of 8°, and finally examined in an R.C.A., type E.M.T. electron microscope at an initial magnification of 3000.

III. Discussion

In the material studied some evidence for the existence of a crossed structure was obtained in *Vinca* (Plate 2, Fig. 1). This evidence is not of itself conclusive but earlier work of Strasburger (1924) has shown that in developing fibres a single set of striations is apparent during the early stages of secondary thickening while in later stages of development, crossed striations are observed. This evidence would thus confirm the presence of the structure in Plate 2, Figure 1. In *Dahlia* no evidence of crossed fibrillar structure was apparent in the end wall of a parenchyma cell (Plate 3) in which extremely small pits measuring about 0.15 by 0.5 μ were noted. In another specimen, however, two distinct directions of orientation of the microfibrils were seen (Plate 4). From the shadow length it was concluded that the upper lamella (transversely oriented in the micrograph) was about 0.1 μ thick. It was concluded that Plate 4 represents the superposition of two adjacent cell walls so that no true crossed structure was present. This is in agreement with Strasburger (1924).

In *Alstonia spathulata* the tracheidal cells in some cases showed definite striations in the cell wall (Plate 1, Figs. 1 and 2). Electron-microscopic examination showed definite crossed fibrillar structure (Plate 5) the microfibrils associating laterally to form banded structures, approximately 0.5 μ in breadth. This tendency had been noted by Frey-Wyssling (1952) and will be discussed further below. In Plate 6 the structure associated with pits can be seen in a whole cell which had collapsed. One of the two pits is in the lower wall and the upper wall is superimposed on it, while the other pit is in the upper wall, and through it can be seen the crossed fibrillar texture of the lower wall. In Plate 2, Figure 2, a fragment of single cell wall similar to that in Plate 1, Figure 2, is shown in which a crossed lamellar as distinct from the cross-banded structure is apparent. In this structure it can be seen that in surface view the upper lamella has an irregular corrugated appearance. The origin of this appearance probably resides in the different directions of shrinkage in the two superimposed lamellae. Thus the major direction of shrinkage will be perpendicular to the direction of orientation of the microfibrils, i.e. the major component of shrinkage in the lower lamella (Plate 2, Fig. 2) will be perpendicular to the microfibril direction in the upper lamella. It is easy to see that this could cause some disorientation in the upper lamella, giving rise to the corrugated appearance observed.

The X-ray diffraction diagram of *Alstonia* consists of two meridional arcs which tend to be resolved into a typical four-point diagram. The spread of the arcs indicates that the micellar strands were oriented at an angle of 60° with respect to the longitudinal cell axis, which agrees well with the run of striations in the cell wall. The major extinction position (m.e.p.) of a single cell wall is approximately transverse, as would be expected if the lamellae were of equal thickness (see, for example, Preston 1952).

In the parenchyma of *Ochroma lagopus* no direct evidence of a crossed lamellar structure was obtained (Plate 7) but the cell walls exhibited the corrugated appearance noted above as associated with this type of structure. The m.e.p. of a single wall, however, did not coincide with the orientation of the pit orifice, which again suggests the probability of a crossed lamellar structure. The pits in Plate 7 measure approximately 1.4 by 0.7 μ in width.

The partially differentiated xylem of *Eucalyptus elaeophora, E. regnans,* and *Ulmus* sp. is shown in Plates 8-11. Considering first the fragment of a vessel element of *E. elaeophora* in Plate 10, a type of irregular crossed structure can be seen which does not, however, resemble that in *Alstonia* as the lateral association of the microfibrils is more limited. Some indication of this type of structure was also apparent in the outer layer of the secondary wall of fibres of *E. elaeophora* (Plate 8) and of *Ulmus* sp. (Plate 11). However, here the position was complicated in that great care was necessary to ensure that the appearance of crossing did not arise from the superposition of two walls of the same cell. Thus the appearance of crossing in Plates 8 and 11 resembles closely that at the left of Plate 9, Figure 1. In the latter, however, which is the outer layer of the secondary wall of *E. regnans,* through the pit aperture can be seen a structure which shows no evidence of crossing, suggesting that the appearance of crossed structure here arises from the superposition of two parts of the same cell wall. Again the fragment of the outer layer of the secondary wall of fibres from *E. elaeophora* in Plate 9, Figure 2, showing no evidence of a crossed structure, apart from the "corrugated" appearance described earlier, was adjacent to that shown in Plate 8. Thus the evidence for the existence of a crossed structure in the outer layer of the secondary wall must be regarded with some doubt, especially as the tendency of microfibrils to associate laterally may lead to spurious effects (see below). However, if present, any crossed structure in the outer layer of fibres and tracheids would appear to correspond most closely with that in vessels (Plate 10).

The survey of the above types of structure leads to the recognition of a cross-banded type of structure as in *Alstonia* tracheids where the microfibrils are associated laterally to form bands about 0.5 μ wide and separated from neighbouring bands by spaces of similar or somewhat smaller breadth and probably occupied by other cell wall constituents. In contrast to this is the crossed lamellar structure seen also in *Alstonia* (Plate 2, Fig. 2) and possibly in the parenchyma of *Ochroma* (Plate 7) where lateral association of the microfibrils is completed to form lamellae.

The association of the microfibrils to form bands seen in Plate 5 provides an excellent example of the phenomenon which has been discussed by Frey-Wyssling (1951). This lateral association of the microfibrils in secondary wall which is absent in primary wall may depend upon the nature of the microfibrils themselves. Thus Frey-Wyssling (1953) has sought to explain the discrepancy in size between the micelles (detected by X-rays) and the microfibrils (detected by the electron microscope) upon the assumption that the microfibril consists of a solid crystalline core surrounded by a paracrystalline cortex, so that only the core would be detected on X-ray examination and the whole structure by the electron microscope. On the other hand it had been proposed (Wardrop 1949) on the basis of the change in apparent micelle size upon acid hydrolysis that the microfibril consists of several micelles, each of which is surrounded by a paracrystalline phase associated with which are various non-cellulosic constituents difficult to extract from the cell wall (see also Sen and Woods 1949). In both views, therefore, the microfibril "surface" consists of paracrystalline cellulose. It is this paracrystalline phase, which on either view would surround the microfibril, which has been proposed by Frey-Wyssling as responsible for the lateral association of microfibrils in banded structures. It is assumed as previously that non-cellulosic substances are associated with the paracrystalline cellulose. Now cleaning for specimen preparation involves some hydrolysis and much of this non-cellulosic material is removed, and there is also an increase in the apparent crystal size as determined by X-rays. This means that the paracrystalline cellulose adds to the size of micelles already present although it does not preclude the formation of some smaller crystalline regions. Such crystallization could give rise to anastomosing connections between bands of microfibrils. This may result, in some cases, in a spurious effect of a crossed fibrillar orientation as in Plate 12, which may be compared with Plates 8 and 11.

In *Alstonia* it would not be surprising, although X-ray evidence is inconclusive, if the strongly hydrophilic 101 planes (6.1 Å spacing) were parallel to the cell surface as in *Valonia* (Preston and Astbury 1937), as suggested for fibres on the basis of X-ray studies during mercerization by Hermans (1949). It would also be consistent with the supposed lath-shaped form of the microfibrils themselves (Preston 1951). In undisturbed regions of the cross-banded and crossed lamellar structures, the angle of intersection of the two directions of orientation is approximately 80°, which is similar to that in *Valonia*. In the regions of pits in *Alstonia* this angle is reduced to about 50° and is also reduced near the tips of fibres in *Ulmus* (Plate 11). This would imply that disturbance of the orientation is cytoplasmic in origin rather than determined by any crystallographic relations between successive lamellae.

The possible existence of a crossed or woven structure in the outer layer of secondary wall of fibres and tracheids requires further consideration because of its technological implications and must be reconciled with the great amount of evidence previously accumulated concerning the organization of this layer. The outer layer of the secondary wall is 0.5-1 μ in thickness in angiosperms and usually about 1 μ in thickness in gymnosperms. The lamellae observed in the electron microscope from their shadow lengths are 0.1-0.2 μ in thickness. Allowing for the presence of non-cellulosic constituents in the intact walls the outer layer probably consists of only two or three lamellae. This may be related to the layered appearance of the outer layer of the secondary wall when delignified and somewhat swollen (Wardrop and Dadswell 1948; Nagatamo 1952).

It is, however, surprising that on crushing single cell walls of tracheids and fibres no evidence is obtained that there exists more than one direction of orientation in the outer layer of the secondary wall (Plate 1, Fig. 3) although in Plate 2, Figure 2, only one orientation direction is apparent except at the edges of the cell wall fragment. In partly differentiated tracheids, however, some evidence of a crossed structure is apparent when examined between crossed nicols (Plate 1, Fig. 5) and when mature tracheids are delignified and examined after drying (Plate 1, Fig. 6). Again the tendency of microorganisms such as fungi (Bailey and Vestal 1937*a*, 1937*b*) to hydrolyse cellulose along preferred planes is well known. This attack usually takes a helical course in the outer layer but some evidence of a tendency for two directions of attack in this layer is apparent in the vessel elements (Wardrop and Dadswell 1952).

Also the growth of iodine crystals in the cell wall (Bailey and Vestal 1937*a*, 1937*b*) usually shows only one direction of helical orientation. On the other hand when fibres or tracheids are greatly swollen to balloon swellings a crossing of the strands arising from the outer layer is sometimes observed and may explain the reluctance of the outer layer to unwind during initial stages of swelling (Wardrop and Dadswell 1950, Figs. 10 and 20).

It is also possible that the difficulty in detecting the contribution of the outer layer of the secondary wall to the X-ray diffraction diagram may arise from the considerable dispersion of the microfibrils about the directions of preferred orientation which is seen in Plate 10 (Preston 1946; Wardrop and Preston 1947; Wardrop 1952).

As previously stated it has been proposed by Bosshard (1952) that a crossed lamellar structure is present in the middle layer of the secondary wall. Although no new evidence has been presented in the present paper there are reasons to suggest that this layer possesses only a simple helical organization (see also Wardrop 1954). Thus a crossed lamellar structure does not appear consistent with the observations of the coincidence of the m.e.p. and striation direction for this layer (Bailey and Berkley 1942), the simple helical form of the fractures occurring in this layer when the cell is broken in tension (Wardrop 1951), or the fact that in compression wood tracheids radial discontinuities exist in the cell wall. All stages of transition between the structure of compression wood tracheids and the structure of normal tracheids exist. As a crossed lamellar structure obviously cannot possess radial discontinuities, this may be regarded as indirect evidence against the occurrence of this structure in the normal wood. The structure of the inner layer of the secondary wall may also be crossed but as yet there is no convincing evidence of this other than its optical properties which are similar to those of the outer layer, and the appearance of delignified tracheids after drying (Plate 1, Fig. 6). This evidence is, however, in no way conclusive.

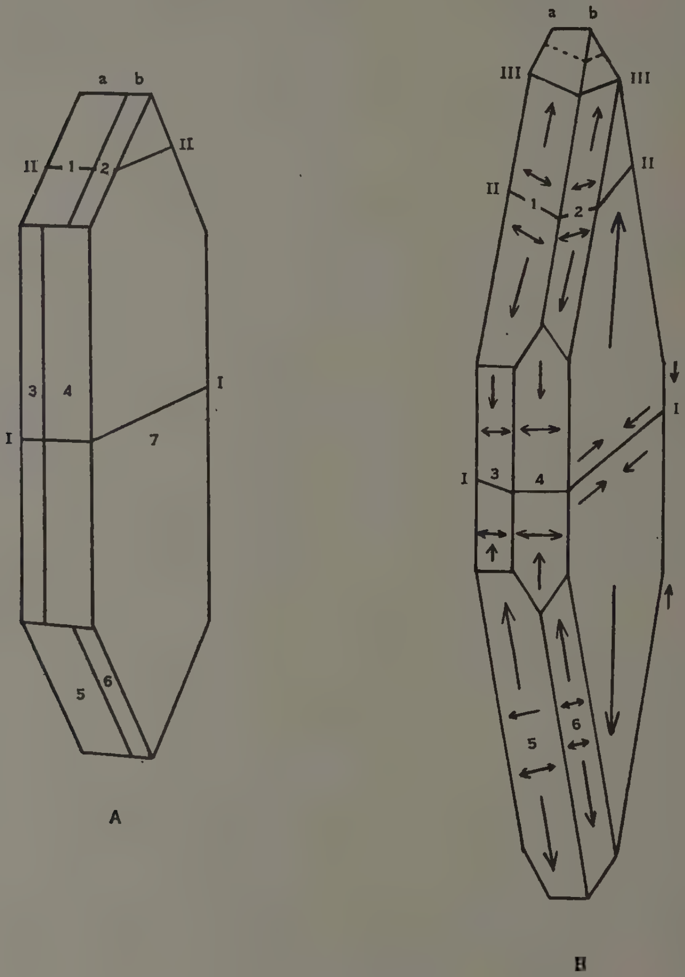


Fig. 1.—Diagrammatic representation of the shape of a cambium initial (*A*) of a mature tracheid (*B*) according to Meeuse (1941). The cell length is reduced 50 times.

In conclusion some reference may be made to the problem of the mechanism governing orientation of the microfibrils in the cell wall. This mechanism undoubtedly resides in the protoplasmic surface (Frey-Wyssling 1948; Preston 1947; Wardrop and Dadswell 1951) since protoplasmic patterns similar to that of the cell wall are often developed prior to secondary cell wall thickening and are particularly apparent when the wall possesses irregular thickening as in the helical thickenings of tracheids, fibres, and vessels. In the present context it is of interest that sometimes two sets of helical thickenings are present, giving rise to a type of crossed structure. It is perhaps significant that the orientation of microfibrils within a cell often appears to be that which might be expected if an elastic body with helical organization were deformed in a particular way. Thus in conifer tracheids it is known that in the middle layer of the secondary wall the microfibrils are oriented at a larger angle to the longitudinal cell axis than are those of the tangential walls (Preston 1934). If now the change in form of a tracheid undergoing differentiation is considered, it can be seen from Figure 1 that there is a change in the relative properties of the different faces with the increase in volume of the cell. The cell elongates, the ends becoming more acute, and the almost rectangular transverse section of the cell becomes approximately hexagonal except at the ends, where it is tetragonal. Thus the original radial walls become considerably wider and the tangential walls narrower (Meeuse 1941). If a simple helical structure were deformed in this way then the observed difference in orientation on the radial and tangential walls would be understandable.

Similarly, in wood fibres as in Plate 11, the orientation is steeper in the narrow "neck" of the fibre than in the "body" of the fibre. A further example of this concerns comparisons between cells of the same origin. Thus in conifer tracheids all derived from the same meristem it is well known that as the length of the cambium initial increases in successive growth rings the angle of micellar orientation with respect to the longitudinal cell axis in the layers of the subsequently formed secondary wall decreases, i.e. the helix steepens. This is just what would be expected if a single helix were progressively stretched (Preston 1934). However, such arguments are usually rejected on the ground that at the time secondary wall formation begins dimensional changes have ceased, at least in that region of the cell where thickening commences. However, this objection need not apply if it is assumed, as Monné has suggested (see Preston 1952), that protoplasmic organization is determined by the cell form and further, in the present case, that it is determined at the inception of secondary thickening, i.e. when the protoplast retracts from the primary wall.

It may here be noted that in the primary wall the protoplast penetrates between the microfibrils and that the microfibrils locally are aligned in the direction of growth, so that in the tips of fibres and tracheids they are approximately parallel to the cell axis (Wardrop 1953).

Thus if the initial protoplasmic surface organization is assumed to be governed by the cell form, this organization will be completed last in those regions of the cell latest in maturing, e.g. the tips of fibres and tracheids, and will be modified by any deformation of the cell in these regions. This initial protoplasmic organization may be regarded thereafter as persisting throughout the life of the cell, provided no major dimensional changes occur. This concept, however, meets a difficulty in attempting to explain the modification of orientation which occurs subsequently as the wall thickens. Thus in tracheids and fibres the helical organization of the secondary wall steepens in the middle layer and again flattens in the inner layer. Changes of this kind may, however, be associated not with cell form but with other factors such as metabolic ones. This view is supported by the observation that both in different fibres and in the cell wall layers of a single fibre a steep micellar orientation is generally associated with a high cellulose content, i.e. with a change in cell metabolism. Thus it is possible that at whatever stage in cell development a thickening layer is developed, it may appear to be related to the cell form although in fact the relationships may be direct only in the initial thickening layer. These questions must, however, remain the subject of speculation for the present, but meanwhile the above considerations may serve as a working hypothesis for our further investigations.

IV. ACKNOWLEDGMENTS

The author is indebted to Mr. J. L. Farrant of the Division of Industrial Chemistry, C.S.I.R.O., and Mr. J. Nicholls of this laboratory for much assistance and advice relating to problems of electron microscopy, and particularly to his colleague, Dr. H. E. Dadswell, for much helpful discussion in the course of the investigation.

V. REFERENCES

ASTBURY, W. T., and PRESTON, R. D. (1940).—*Proc. Roy. Soc.* B **129**: 54.

BAILEY, I. W., and BERKLEY, E. E. (1942).—*Amer. J. Bot.* **29**: 231.

BAILEY, I. W., and VESTAL, M. R. (1937*a*).—*J. Arnold Arbor.* **18**: 185.

BAILEY, I. W., and VESTAL, M. R. (1937*b*).—*J. Arnold Arbor.* **18**: 196.

BOSSHARD, H. H. (1952).—*Ber. schweiz. bot. Ges.* **62**: 482.

FREY-WYSSLING, A. (1951).—*Holz. a. Roh-u. Werkst.* **9**: 333.

FREY-WYSSLING, A. (1952).—"Submicroscopic Morphology of Protoplasm." (Elsevier: Amsterdam.)

FREY-WYSSLING, A. (1953).—Thirteenth International Congress of Pure and Applied Chemistry. Abstracts of Papers. I.U.P.A.C., Stockholm.

HERMANS, P. H. (1949).—"Physics and Chemistry of Cellulose Fibres." (Elsevier: Amsterdam.)

HODGE, A. J., and WARDROP, A. B. (1950).—*Aust. J. Sci. Res.* B **3** (3): 265.

ITERSON, G. VAN (1933).—*Chem. Weekbl.* **30**: 1.

MEEUSE, A. D. J. (1941).—*Rec. Trav. Bot. Néerl.* **38**: 20.

NAGATAMO, S. (1952).—*Bot. Mag., Tokyo* **65** (43): 765.

NICOLAI, E., and FREY-WYSSLING, A. (1938).—*Protoplasma* **30**: 401.

PRESTON, R. D. (1934).—*Phil. Trans.* B **224**: 131.

PRESTON, R. D. (1946).—*Proc. Roy. Soc.* B **133**: 327.

PRESTON, R. D. (1947).—*Proc. Roy. Soc.* B **134**: 202.

PRESTON, R. D. (1951).—*Disc. Faraday Soc.* **11**: 165.

PRESTON, R. D. (1952).—"Molecular Architecture of Plant Cell Walls". (Chapman Hall: London.)

PRESTON, R. D., and ASTBURY, W. T. (1937).—*Proc. Roy. Soc.* B 122: 76.

PRIESTLEY, J. H., SCOTT, L. I., and MALINS, M. (1933).—*Proc. Leeds Phil. Lit. Soc.* (Sci. Sect.) 2: 365.

SACHS, J. (1882).—"Textbook of Botany". (Oxford.)

SEN, M. K., and WOODS, H. J. (1949).—*Biochim. Biophys. Acta* 3: 510.

STRASBURGER, E. (1924).—"Practical Botany". 8th Ed. (Allen and Unwin: London.)

STRASBURGER, E. (1930).—"Textbook of Botany." 6th English Ed. (Macmillan: London.)

WARDROP, A. B. (1949).—*Nature* 164: 366.

WARDROP, A. B. (1951).—*Aust. J. Sci. Res.* B 4 (4): 391.

WARDROP, A. B. (1952).—*Text Res. J.* 22 (4): 288.

WARDROP, A. B. (1954).—*Aust. J. Bot.* 2: 165.

WARDROP, A. B. (1954).—*Holzforschung* (in press).

WARDROP, A. B., and DADSWELL, H. E. (1948).—*Aust. J. Sci. Res.* B 1 (1): 3.

WARDROP, A. B., and DADSWELL, H. E. (1950).—*Proc. Aust. Pulp Ind. Tech. Ass.* 4: 198.

WARDROP, A. B., and DADSWELL, H. E. (1951).—*Nature* 168: 610.

WARDROP, A. B., and DADSWELL, H. E. (1952).—*Aust. J. Sci. Res.* B 5 (2): 223.

WARDROP, A. B., and PRESTON, R. D. (1947).—*Nature* 160: 911.

DESCRIPTION OF PLATES 1-12

All electron micrographs (Plates 2-12) were taken at an initial magnification of 3000 after uranium shadowing.

PLATE 1

Fig. 1.—*Alstonia spathulata.* A tracheid from an aerial root showing pits and cell wall striations (cf. Plate 6). Phase contrast × 680.

Fig. 2.—*Alstonia spathulata.* A fragment of the cell wall of a tracheid from an aerial root showing pits and crossed striations. (cf. Plate 2, Fig. 2). Phase contrast × 1000.

Fig. 3.—*Pinus radiata.* A single cell wall of a tracheid after staining with congo red and gentle crushing. Note the opposed striation directions. × 980.

Figs. 4, 5.—*Pinus radiata.* Two partly differentiated tracheids, showing in *A* only the primary wall, and in *B* the outer layer of the secondary wall. Note the striations in *B*. Figure 5 photographed between crossed nicols. × 1000.

Fig. 6.—*Pinus longifolia.* A single cell wall after delignification and drying. Note the striations. × 450.

PLATE 2

Fig. 1.—*Vinca major.* A fragment of the secondary cell wall showing crossing of microfibrils. Longitudinal cell axis horizontal. × 16,000.

Fig. 2.—*Alstonia spathulata.* A fragment of a tracheid showing crossed lamellar structure. Longitudinal cell axis lower left to upper right; compare Plate 1, Figure 2. × 21,000.

PLATE 3

Dahlia sp. Part of the cell wall of a parenchyma cell from the pith of a tuber. × 16,000.

PLATE 4

Dahlia sp. Showing two adjacent cell walls of pith parenchyma. × 16,000.

PLATE 5

Alstonia spathulata. Cross-banded structure in the cell wall of a tracheid. Longitudinal cell axis approximately diagonal. × 16,000.

PLATE 6

Alstonia spathulata. Part of a whole cell showing two pits (see text) in cross-banded structure. Longitudinal cell axis horizontal. × 17,000.

PLATE 7

Ochroma lagopus. Part of a parenchyma cell wall showing pits. Longitudinal cell axis vertical. × 17,000.

PLATE 8

Eucalyptus elaeophora. Part of the outer layer of the secondary wall showing supposed crossed fibrillar structure. Longitudinal cell axis vertical. × 18,000.

PLATE 9

Fig. 1.—*Eucalyptus regnans.* Part of the outer layer of the secondary wall with a pit orifice. Longitudinal cell axis horizontal. × 16,000.

Fig. 2.—*Eucalyptus elaeophora.* Part of the outer layer of the secondary wall adjacent to that shown in Plate 8. Longitudinal cell axis vertical. × 16,000.

PLATE 10

Eucalyptus elaeophora. Part of the cell wall of a vessel with a pit communicating with a ray. Note the crossed structure in the cell wall. Longitudinal cell axis horizontal. × 15,000.

PLATE 11

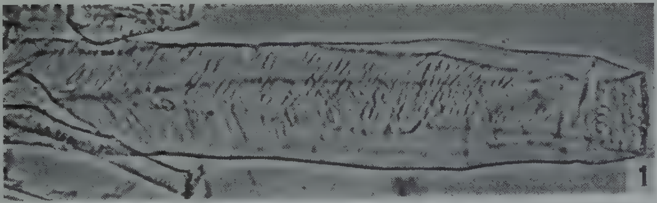
Fig. 1.—*Ulmus* sp. The tip of a fibre showing supposed crossed fibrillar structure in the outer layer of the secondary wall. Longitudinal cell axis vertical. × 10,000.

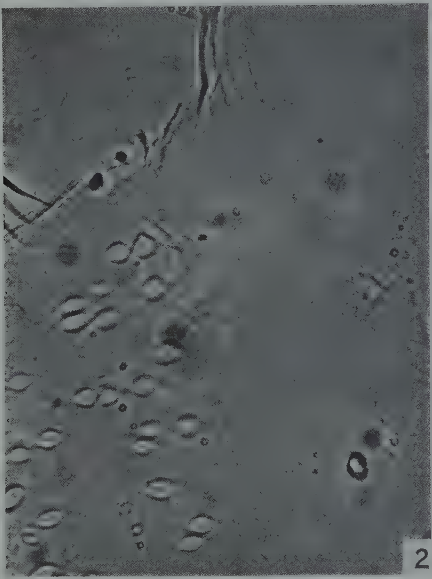
Fig. 2.—*Ulmus* sp. As Figure 1 further from the cell tip. × 10,000.

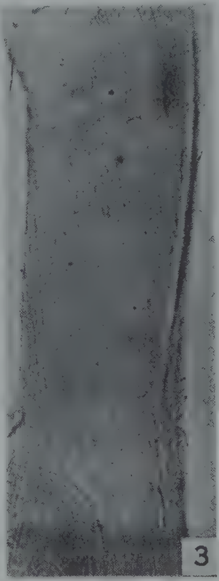
PLATE 12

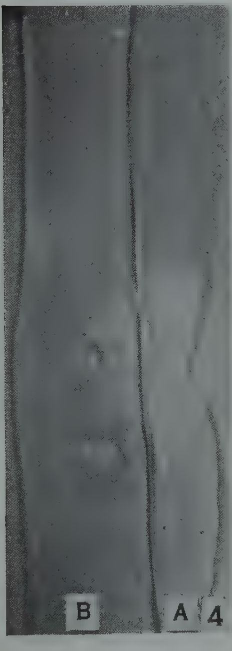
Eucalyptus elaeophora. Part of the secondary wall, probably the outer layer, showing lateral association of microfibrils and spurious crossed fibrillar structure (see text). × 22,000.

CROSSED LAMELLAR STRUCTURES IN CELL WALLS

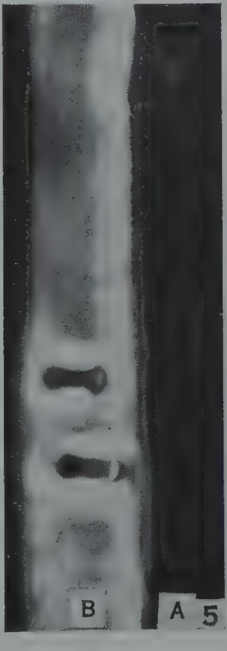

1


2

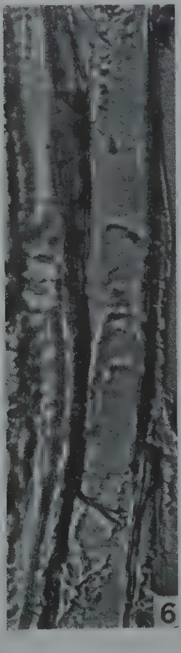

3



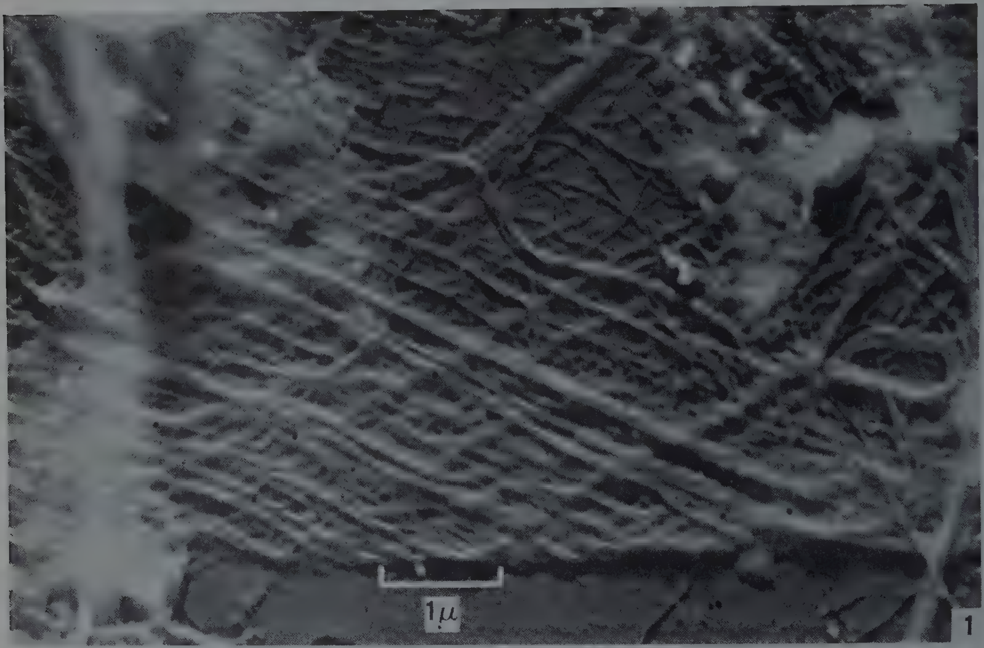
4



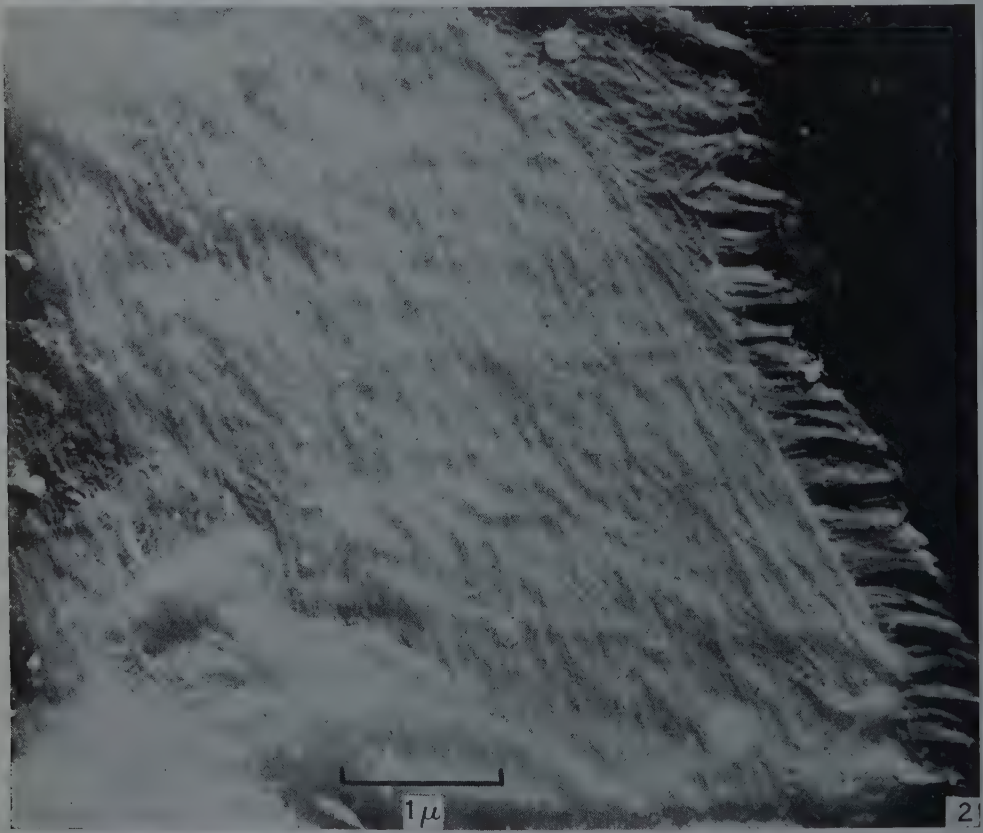
5


6

CROSSED LAMELLAR STRUCTURES IN CELL WALLS

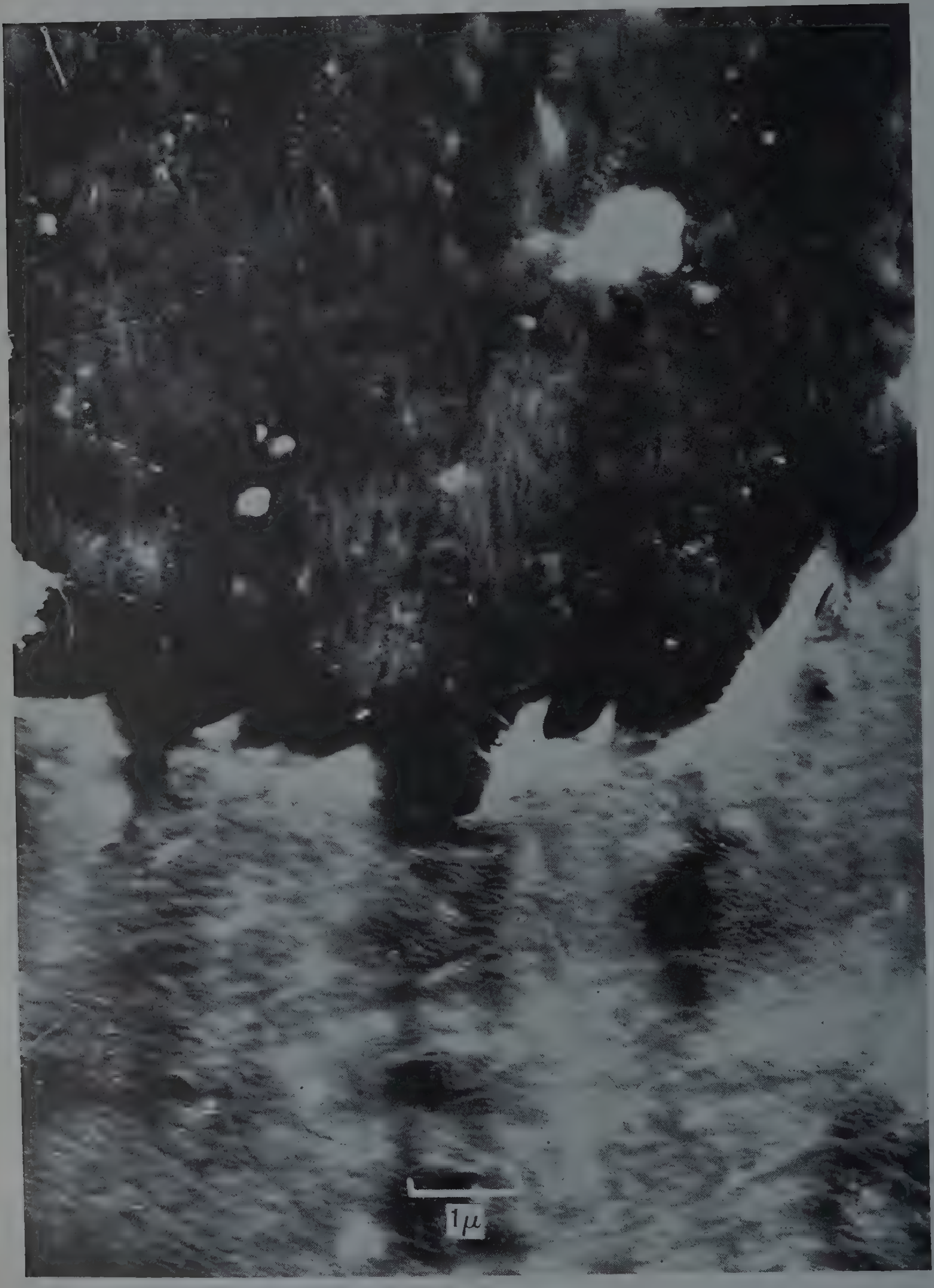


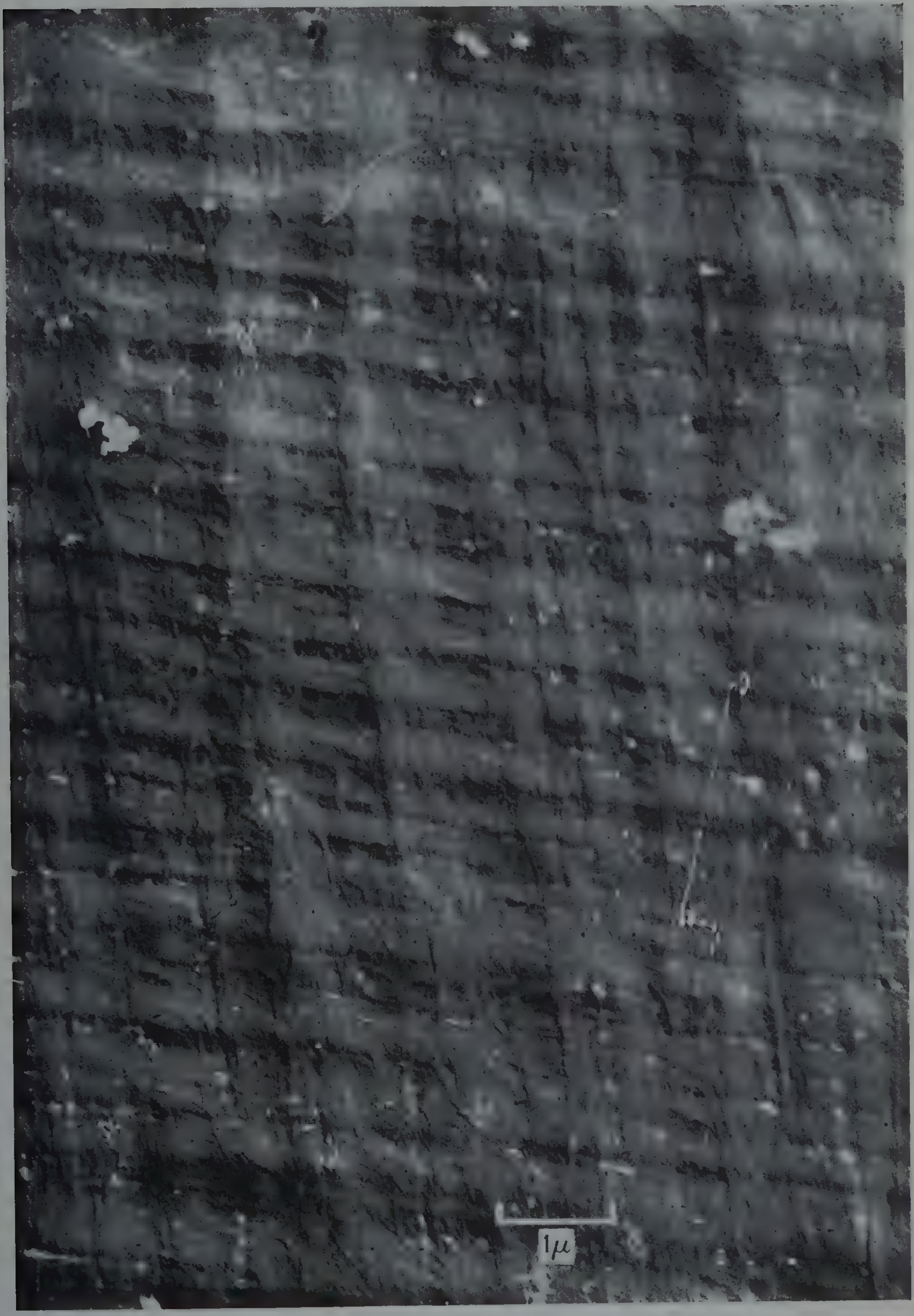
1

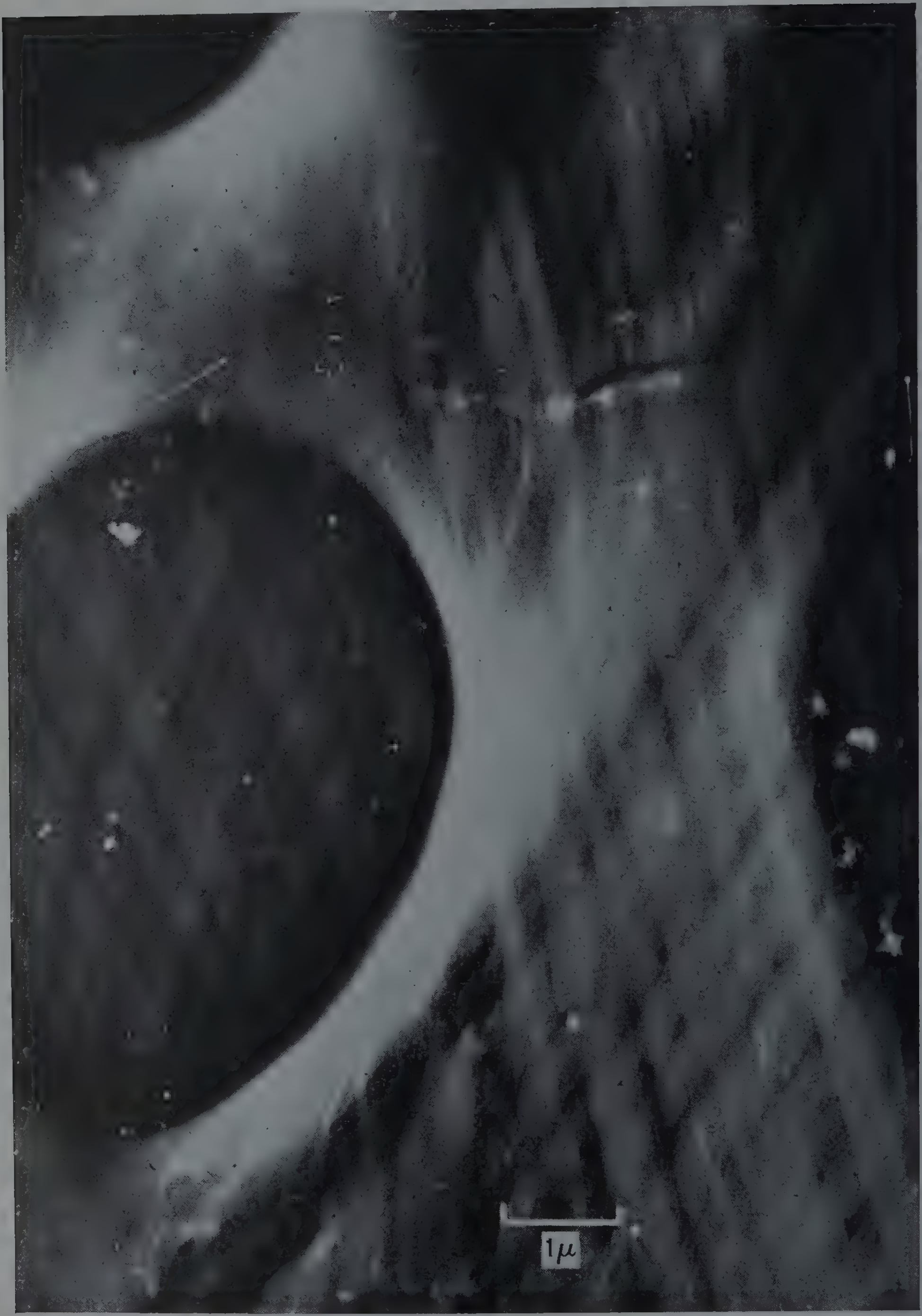


2

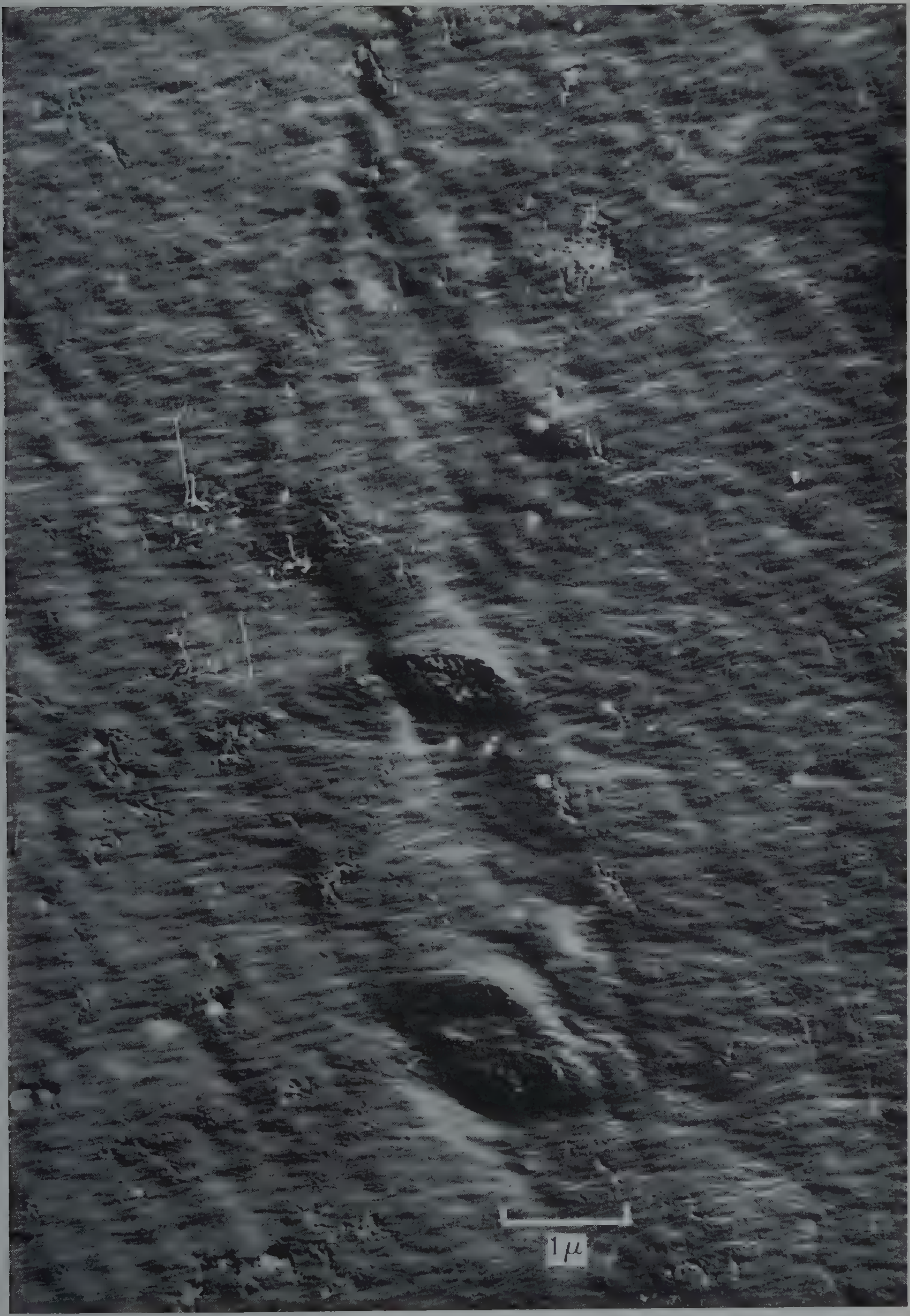
CROSSED LAMELLAR STRUCTURES IN CELL WALLS


1μ

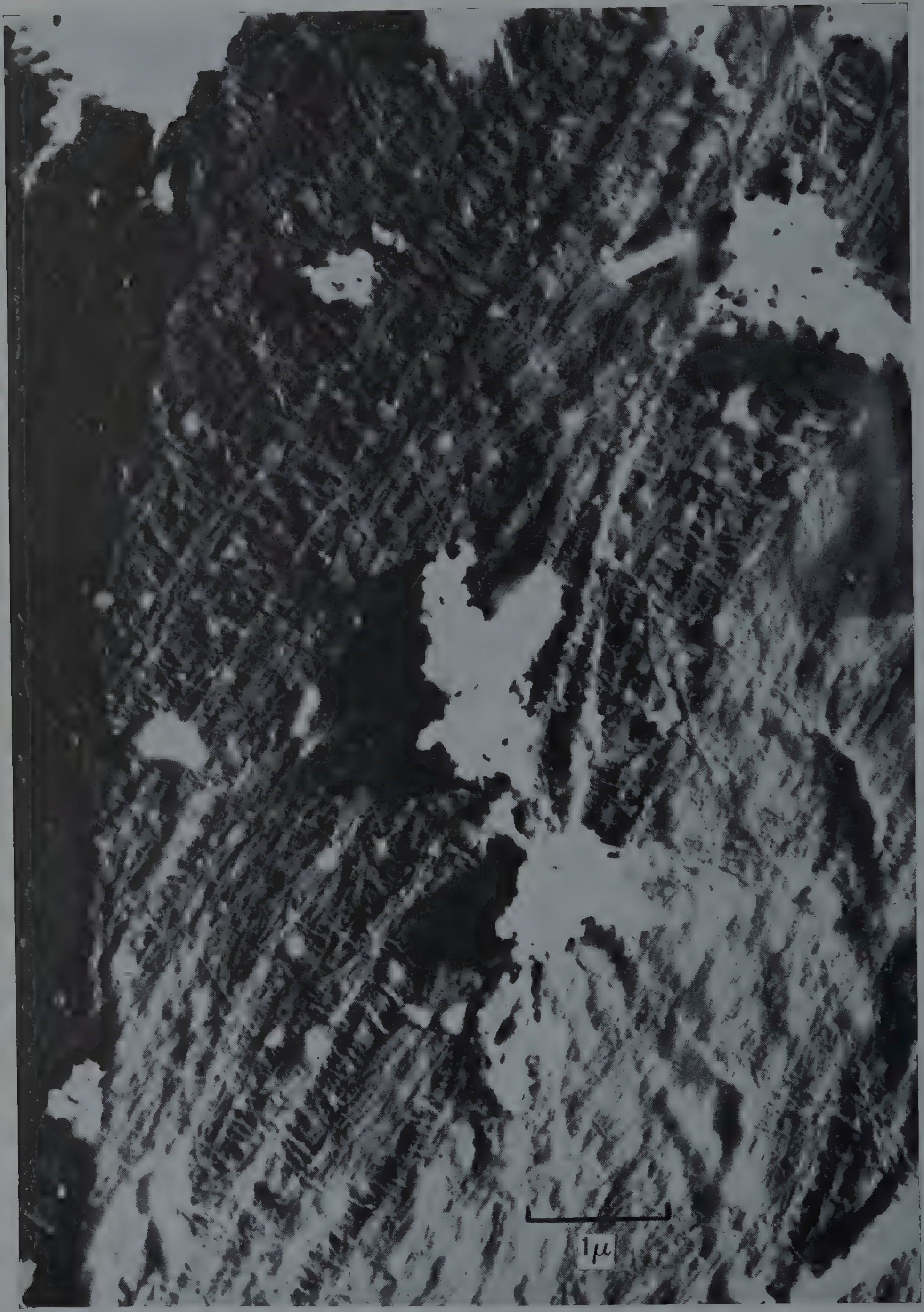

1μ


1μ

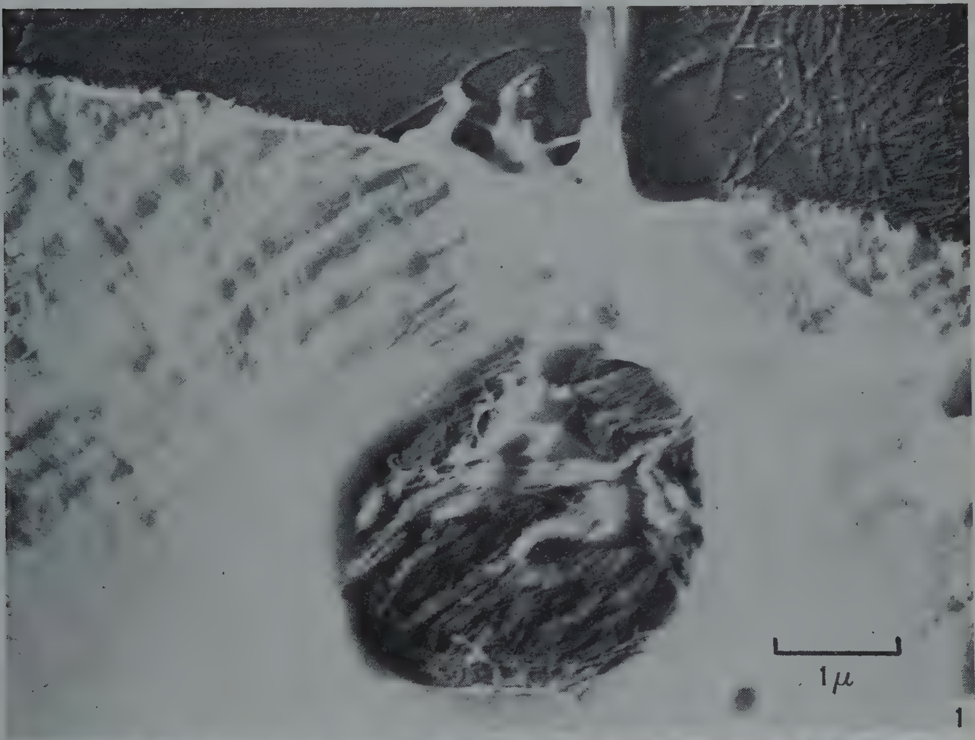
CROSSED LAMELLAR STRUCTURES IN CELL WALLS



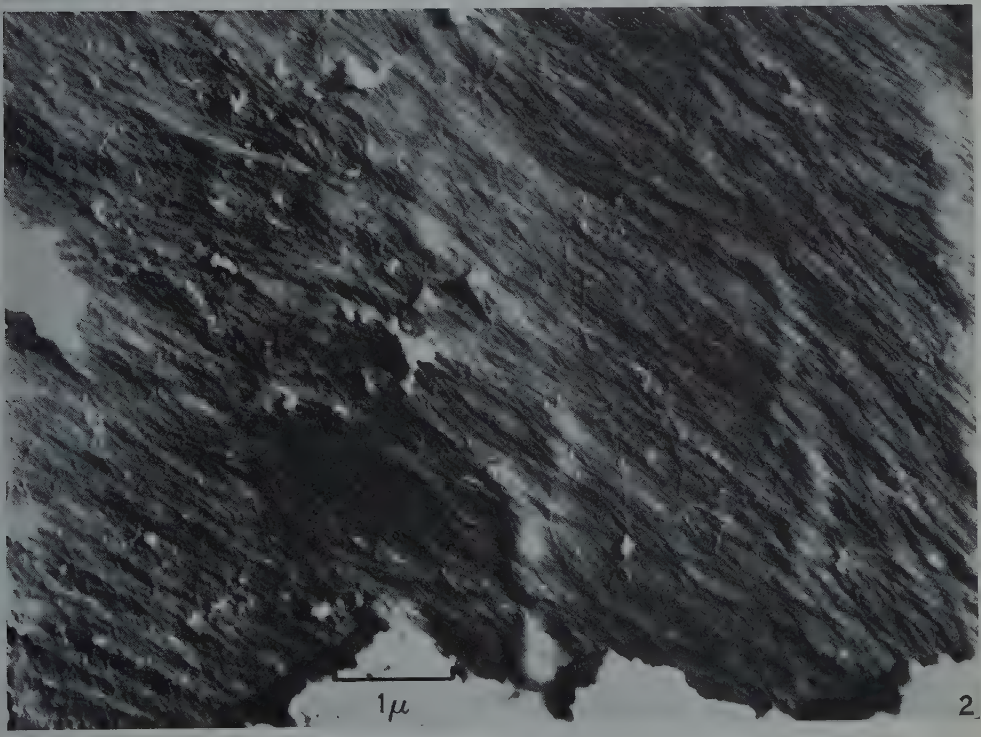
CROSSED LAMELLAR STRUCTURES IN CELL WALLS



CROSSED LAMELLAR STRUCTURES IN CELL WALLS

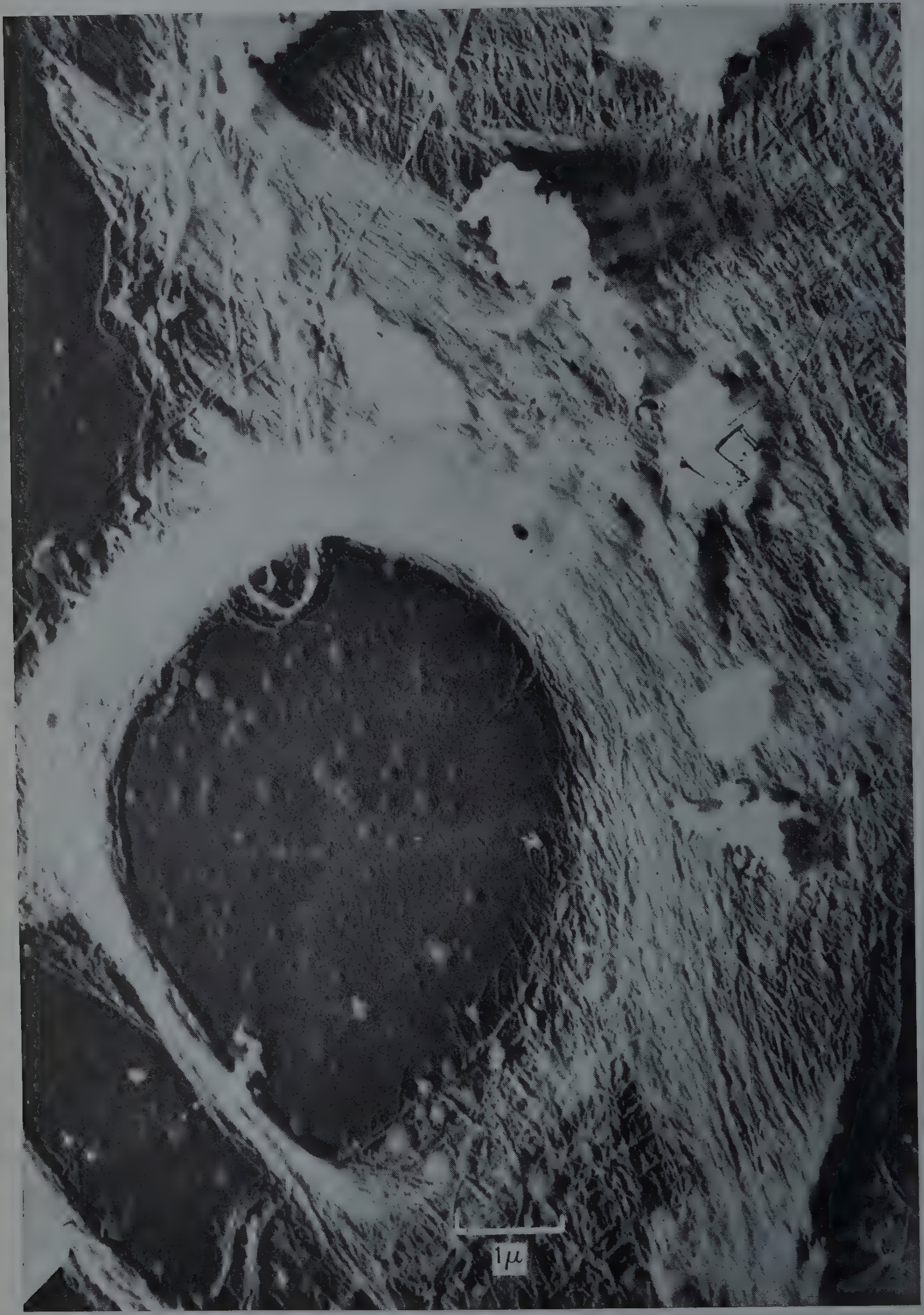


1

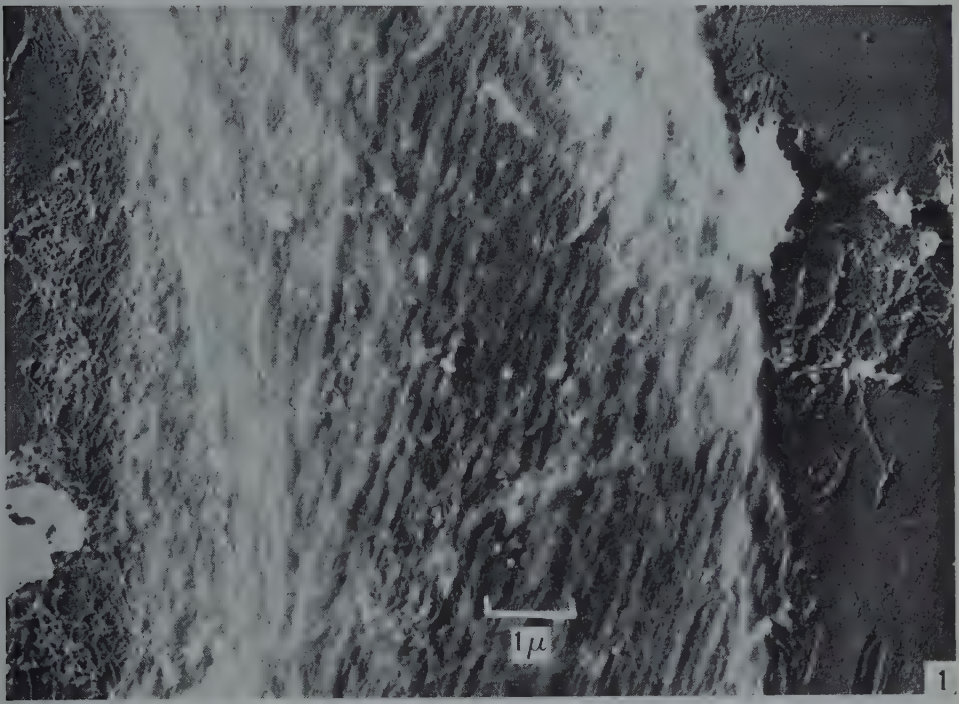


2

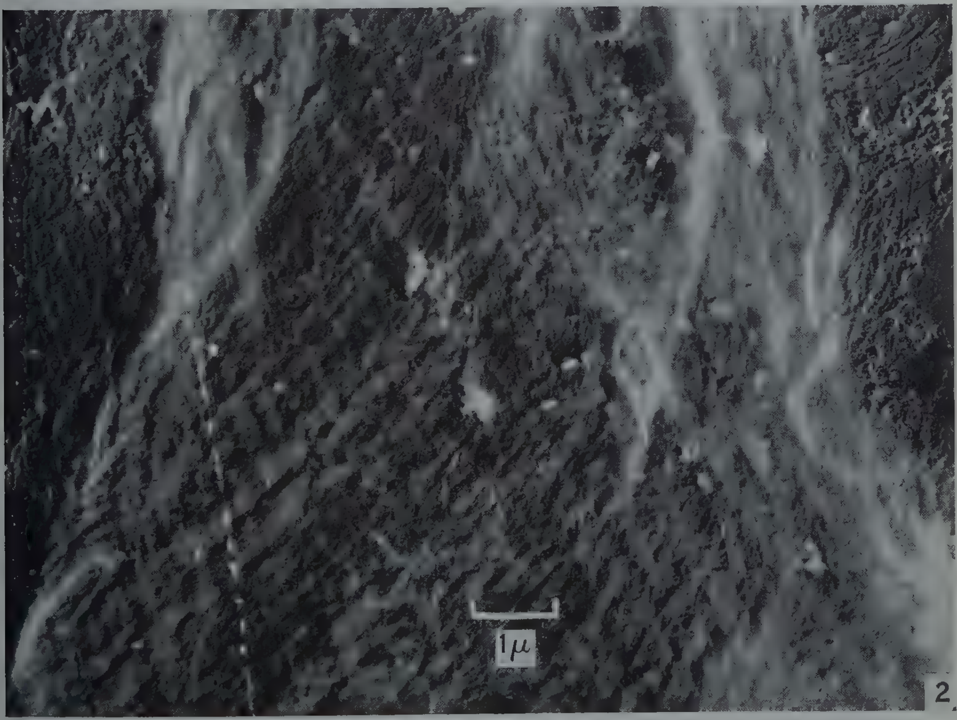
CROSSED LAMELLAR STRUCTURES IN CELL WALLS



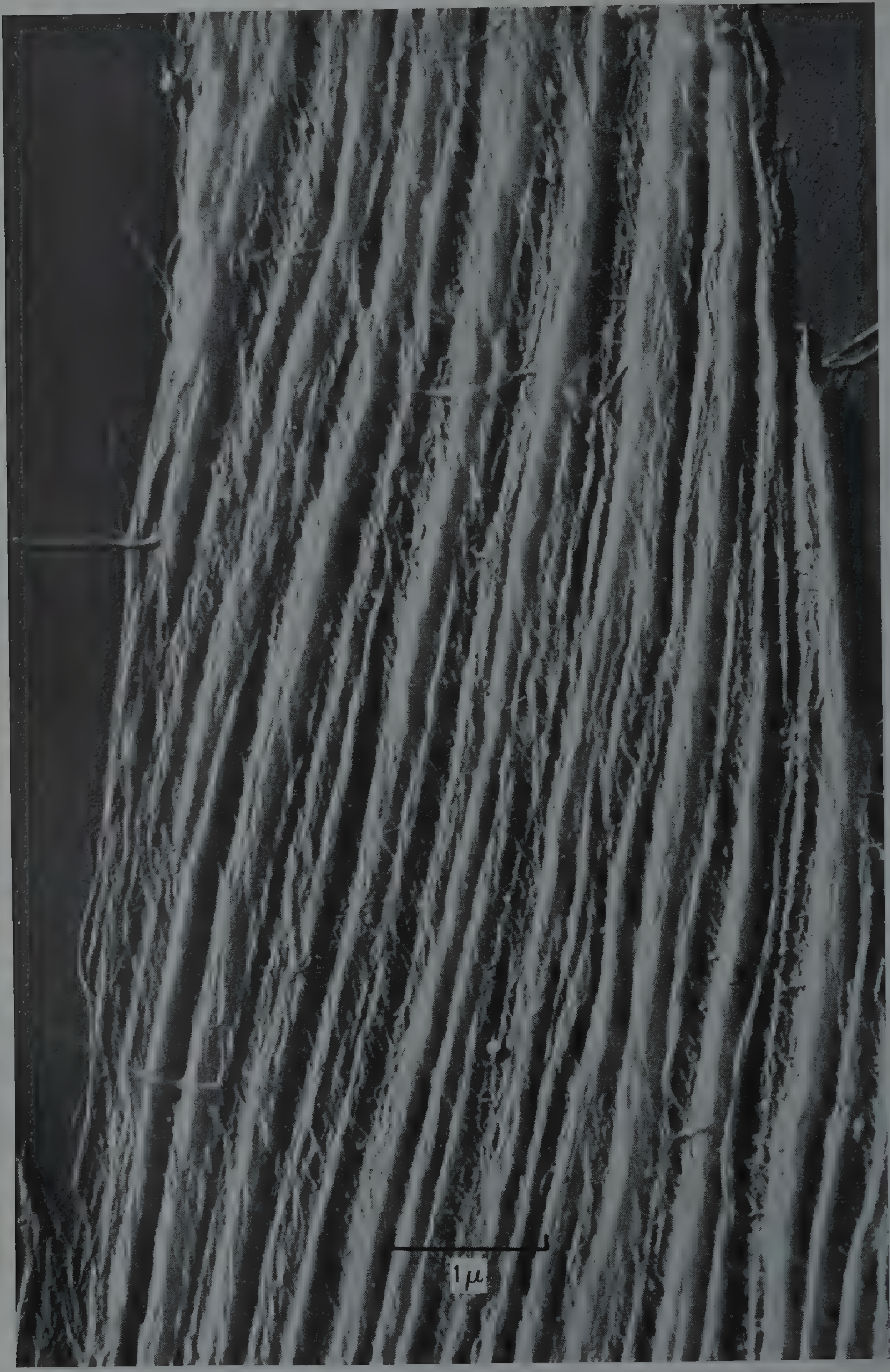
CROSSED LAMELLAR STRUCTURES IN CELL WALLS



1



2


1 μ

THE MECHANISM OF SURFACE GROWTH INVOLVED IN THE DIFFERENTIATION OF FIBRES AND TRACHEIDS

By A. B. Wardrop*

(*Manuscript received February* 15, 1954)

Summary

An electron microscopic investigation has been made of the differentiating xylem elements of *Pinus radiata*, *Eucalyptus elaeophora*, and *Ulmus* sp. In the tips of fibres and tracheids there is a tendency for the microfibrils of cellulose to be oriented in the direction of growth. It is considered that this orientation can be disturbed by subsequent dimensional changes in the cell. The thin areas of the differentiating cells which are involved in the so-called "mosaic growth" have been compared with the regions of the cell wall penetrated by plasmodesmata in the storage parenchyma of potato tubers. The suggestion is made that the thin areas are regions of the cell wall penetrated by plasmodesmata, or are developing primary pit fields. The implications of this concept, with respect to intercellular readjustment and to the differences between fibres and tracheids in extension growth, are discussed.

I. Introduction

The mechanism of dimensional changes involved in the differentiation of fibres and tracheids from the cambium is of particular interest since not only do the daughter cells increase in length, but also in breadth, so that the process is considerably more complex than where pure extension growth is involved, e.g. in the parenchyma of coleoptiles.

Investigation of the cell wall organization of conifer cambium by optical (Kerr and Bailey 1934; van Iterson 1935), X-ray (Preston and Wardrop 1949), and electron-microscopic techniques (Hodge and Wardrop 1950) served to establish the existence of a dispersed texture, in which the mean direction of orientation of the cellulose microfibrils was approximately transverse to the longitudinal cell axis. This had been shown previously in the primary walls of other elongated cells (Frey-Wyssling 1936).

The fibres of angiosperms elongate 100-500 per cent. and increase in radial breadth 50-200 per cent. (Bailey 1920). In the view of Schoch-Bodmer and Huber (1952), this increase in length is effected by interposition growth (intrusive growth of Sinnott and Bloch (1939)) in which growth was considered to be confined to the cell tip. In the body of the cell, no longitudinal growth was supposed to occur. This was correlated with the absence of pits near fibre tips, and appeared to explain more adequately the diversity of shape of fibres after differentiation than the concept of symplastic growth proposed by Priestley (1930) which was subsequently supported by Meeuse (1941*a*).

---

* Division of Forest Products, C.S.I.R.O., South Melbourne.

The increase in length of conifer tracheids during differentiation is less than with angiosperm fibres, being only 5-20 per cent., but the increase in breadth is 200-500 per cent. (Bailey 1920). Although detailed arguments have been formulated supporting the view of symplastic growth, the recent work of Bannan (1950) has again suggested that growth is confined to the cell tips; and similar evidence to that used by Schoch-Bodmer in support of interposition growth in fibres has been presented for tracheids by Wardrop and Dadswell (1952). However, in tracheids, pits are often found near the tips, and indeed may tend to be concentrated there (Bannan and Whalley 1950).

The mechanism of tip growth in parenchyma has been discussed by Mühlethaler (1950) and by Frey-Wyssling (1952). It was considered that the cytoplasm extruded through the tip of an extending cell and softened the middle lamella in front of it. This recalls the earlier suggestion of Neeff (1914) that the middle lamella is dissolved by the extending cell tip. On the other hand, the surface growth of the cell, apart from tip growth, was considered to take place by means of the so-called "mosaic" growth (Frey-Wyssling and Stecher 1951; Stecher 1952), which has been discussed by Bosshard (1952) in relation to the differentiation of wood fibres. According to this concept, the cell surface is enlarged by a localized synthesis of cytoplasm penetrating the wall, which loosens the meshwork of microfibrils of the cell wall at localized points which are subsequently closed in again with new microfibrils.

While these concepts throw great light on our present views of the nature of intercellular readjustment in tissues, it seemed that some further investigation was needed, particularly the manner in which cell growth in a tissue is coordinated, and what differences exist between fibres and tracheids in extension growth during differentiation. With these points the present paper is concerned.

II. Materials and Methods

Using the method of Priestley, Scott, and Malins (1933), differentiating xylem was collected for examination from *Pinus radiata* D. Don, *Eucalyptus elaeophora* F. Muell., and *Ulmus* sp.

The material was treated in two ways:

(*a*) Extracted with 5 per cent. sodium hypochlorite for 24 hr at room temperature, then given alternate extractions with boiling 1 per cent. sodium hydroxide and boiling 1 per cent. hydrochloric acid, and finally vigorously shaken to effect maceration.

(*b*) Extracted with alkali and acid as in (*a*) and then disintegrated in a mechanical disintegrator.

In addition, the parenchyma of potato tubers was examined to study the anatomy of the cell wall in the region of plasmodesmata (see Section III). A portion of the tuber was treated as in (*b*) above.

A drop of the cell suspension was placed on collodion-covered grids, shadowed with uranium, and examined in an R.C.A. type E.M.T. electron microscope at an initial magnification of 3000 X.

III. Results and Discussion

Frey-Wyssling (1952), discussing the mechanism of tip growth of cells, referred to the tendency of the microfibrils to be parallel to the cell axis near the cell tips, but in the body of the cell to have both longitudinal and transverse orientations. He concluded that there was first formed a "warp" into which was subsequently incorporated a "weft" of transversely oriented microfibrils. The tendency to both orientations in the central part of tracheids and fibres is shown in Plates 1 and 3. At the tips of the cells (Plate 2, Fig. 1; Plate 4), longitudinally oriented microfibrils are seen to extend backwards a distance of some microns, much further than is apparent in the electron micrographs presented by Frey-Wyssling (1952). This gives rise to the question as to whether the "warp" and "weft" of microfibrils are to be regarded as two distinct orientations of separate origin, or whether the weft arises during change of cell shape from a distortion of the "warp". Thus, in a cell such as that in Plate 4, transversely oriented microfibrils were present near the "shoulder", i.e. the region supposed by Schoch-Bodmer not to be involved in cell extension. If it is assumed that the microfibrils develop and are oriented in the direction of growth, for which there is some evidence (Wardrop and Dadswell 1951), then the existence of a tendency to parallel orientation at the cell tip is to be expected. Furthermore, the region of parallel orientation would be shorter in cells undergoing relatively slight extensions, as in tracheids or sieve tubes, than in cells undergoing considerable extension, as in fibres. Accepting this view, the pattern of orientation of the microfibrils would be expected to depend not only on the degree of extension of the cell in any direction, but also upon the sequence of changes taking place. Thus, if the differentiating xylem extended in length before increasing in radial breadth, as illustrated for *Sparmannia* by Schoch-Bodmer and Huber (1952), little axial orientation of the microfibrils in the primary wall would persist. However, examination of differentiating xylem of *Robinia*, in which the fibres possess a well-defined shoulder, shows that the intruding tips of the fibres do not become apparent until radial dimensional changes are well advanced, as has been illustrated by Eames and MacDaniels (1947). It is reasonable to conclude that increases in cell length and radial breadth proceed, at least in part, simultaneously, which is consistent with orientations observed. Thus it cannot be said with any certainty that in tip growth there are two orientations of separate origin as proposed by Frey-Wyssling, but rather that the existing orientations in the primary wall are to be regarded as an expression of the cell shape.

A feature of the terminal regions of fibres and tracheids early in development is the absence of any thin areas such as those shown in Plate 3 which are similar to areas observed in other tissues by Frey-Wyssling and Stecher (1951). These were apparent in the body of the cell in *Eucalyptus elaeophora* where they measured about 1 by 0.5 μ, but in *Pinus radiata* had a somewhat different appearance (Plate 2, Fig. 2), and in some instances there was an asymmetrical build-up of microfibrils on one side (Plate 7, Fig. 1). If these thin areas are visualized as they exist in the living cell, they must represent concentrated zones of cytoplasm, or of non-cellulosic constituents, or of both. Now, in terms of Frey-Wyssling and Stecher's concept of mosaic growth, the development of thin areas involving the localized displacement of microfibrils must result in some slip between surface elements of adjacent cells. Furthermore, the thin areas are often *c.* 1 μ in width, so they should be recognizable in the optical microscope. However, the only structures of this order of size seen under these conditions in the cell wall were the plasmodesmata and primary pit fields, and the idea thus arose that the thin areas participating in mosaic growth might be identical with such structures. Accordingly, for comparison, the examination of a tissue in which plasmodesmata were numerous was undertaken. For this purpose, the storage parenchyma of potato was selected (Crafts 1933). In Plate 5, thin areas, *c.* 0.5 μ in diameter and of varying degrees of looseness of texture can be seen, whereas in Plate 6 larger areas, as well as areas similar to those in Plate 5, are present. In Plate 7, Figure 2, even larger thin areas than those in Plate 6 can be seen. Undoubtedly, the larger areas in Plate 6 and Plate 7, Figure 2, are primary pit fields, and it is reasonable to conclude that the small areas of Plate 5 are regions of the cell wall formerly penetrated by single protoplasmic strands. All of these areas are essentially similar to those shown in Plate 3. Thus, anatomically, there is no objection to the assumption that the thin areas, supposed by Frey-Wyssling and Stecher to participate in mosaic growth, and the regions of penetration of the cell wall by plasmodesmata are identical.

However, whether this identity of the structures is accepted or not, a further more fundamental question must be answered. Thus, does the recognition of thin areas in the primary cell wall of itself constitute any evidence that growth proceeds by a mechanism such as that contained in the concept of mosaic growth? In the absence of direct observation, confirmation of such an assumption must be sought in the distribution of plasmodesmata and other features of the minute anatomy of the cells in relation to the cell growth; so that some further consideration may now be given to the nature of plasmodesmata and primary pit fields, both regarding their distribution and form.

In considering the development of plasmodesmata, Meeuse (1941*b*) concluded that the most plausible mechanism of their origin is that initially the primary wall is completely penetrated by the protoplast, adjacent protoplasts thus being in contact over their entire surface, but later the protoplast extricates itself from the wall and remains in communication only in certain regions—the plasmodesmata. This view corresponds closely with that of Frey-Wyssling (1952) regarding cell wall development, namely that the protoplast in a developing cell permeates the wall only in localized areas. Now, as cell growth involves a great increase in protein synthesis as well as uptake of water and nutrients, it can be seen that enlargement of one cell must, in some degree, invoke expansion in adjacent cells, so that adjacent walls with plasmodesmata would be expected to grow in unison, unless the growth in one cell was so rapid as to break protoplasmic contact with adjacent cells. This might occur, for example, in the differentiation of vessels, but, apart from this, the existence of gradients of form and development of cells connected by plasmodesmata is understandable.

This concept of coordinated growth between cells by means of plasmodesmata appears consistent with the picture of cell elongation in the much simpler case of the root investigated by Sinnott and Bloch (1939), who describe the process as follows: "The lengthening of the tissue can best be pictured as due not to successive increase in one cell after another but rather to the progressive elongation of the entire series of cell walls, sweeping up from the base towards the apex of the root and affecting all the walls at a given level equally, regardless of what cells these happen to form a part". This process is considered by Sinnott and Bloch to differ only in degree from that taking place in cells differentiating from lateral meristems such as cambium. This concept, in which growth is considered to be a function of the tissue as a whole, rather than of the individual cells composing it, recalls the earlier view of Sachs (1878, 1879), that growth in a tissue is primary and cell division and disposition of cell walls secondary.

What may be further expressions of this coordinated growth between cells may be found in the well-known examples of the correspondence between cells of lines of cellulose thickening, such as annular thickenings in protoxylem, and the reticulate thickenings in regenerating vessels of *Coleus* (Sinnott and Bloch 1945). Thus if the thickenings arise in the areas of the wall not penetrated by plasmodesmata, then, because of the coordinated growth between cells, the correspondence in pattern between adjacent cells could be expected.

Obviously, in the surface enlargement of the cell wall, an attenuation of the microfibrillar network must occur. That this occurs in localized areas is the essential point of Frey-Wyssling and Stecher's (1951) concept of mosaic growth. In terms of the views expressed above, the cell surface must be increased by an enlargement of the cytoplasm in the plasmodesmata. This may then be followed by a peripheral encroachment of, or a subdivision of, the plasmodesmata by the synthesis of new microfibrils. What appears to be a feasible picture of the mechanism is presented in Figure 1. This agrees essentially with the proposals of Frey-Wyssling and Stecher, but the growth points are considered to have greater permanency, i.e. the cycle of enlargement due to cytoplasmic synthesis and formation of microfibrils may continue a number of times.

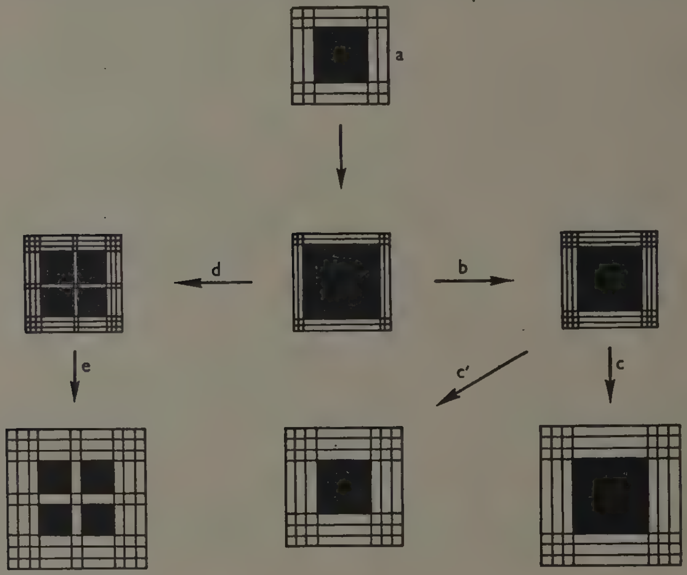


Fig. 1.—A diagrammatic representation of a possible mechanism of surface enlargement of the plant cell. Two directions of orientation of the microfibrils are assumed.
a, Phase of synthesis of cytoplasm (black), pushing aside the microfibrils.
c, Surface enlargement separating the new microfibrils.
b, The incorporation of new microfibrils.
c^1, In this case the possibility that the enlarged area of the cytoplasm is not maintained is shown.
d-e, Similar mechanisms to those shown in *a-c* but involved in the development of a primary pit field.
It is not considered that the phases *a-c* are necessarily consecutive.

It is not considered essential that growth should be symmetrical, as shown in Figure 1—indeed the thin areas are often elongated (Plate 3)—nor must it be assumed that all areas are active at the same time. The possibility of plasmodesmata being divided by cellulosic strands (Meeuse 1941*b*) to form groups may also be involved in surface enlargement (Plate 6; Plate 7, Fig. 2; Fig. 1).

In Plate 6 and Plate 7, Figure 2, it can be seen that, at the stage of cytoplasmic synthesis (Fig. 1*b*), there is a tendency for the microfibrils to be arranged peripherally around a thin area. This is particularly of interest in Plate 7, Figure 1, where the build-up of microfibrils between two thin areas is apparent. It is probable that these are crassulae which have been said to represent the remains of thicker parts of the cambium wall between primary pit fields which are visible in the optical microscope. The thin area—*A*—in Plate 7, Figure 1, is approximately the size of a primary pit field in *Pinus radiata*. This is described further below.

What may be regarded as a special and most important case of this correspondence of secondary thickening between cells is the development of pits. These structures are well recognized to develop in the region of primary pit fields, although all primary pit fields do not necessarily give rise to a pit.

Now particularly in the xylem of conifers, pits are confined almost exclusively to the radial walls. If, as the above considerations would imply, pits are to be regarded as defining areas which have been regions of wall growth, then the observed distribution is quite understandable. Further, pits are known to be more frequent towards the tips of conifer tracheids (Bannan and Whalley 1950)—regions where growth in length is greater. In contrast to this, in fibres of angiosperms, pits appear to be less frequent towards the tips. In this connection several points must be considered, such as the intercellular readjustment of the initials which takes place following division in the cambium, and the dimensional changes of the cell which occur during differentiation. It is reasonable to suppose, as is usually done (Meeuse 1941*b*; Bannan and Whalley 1950), that in new intercellular contacts, occurring after division, new plasmodesmata may be formed. By surface growth in these regions, some extracambial elongation may take place, although it would appear that most of this elongation is effected by tip growth. This would appear to be the case particularly in angiosperm fibres where extracambial elongation is greatest and pits are less frequent or absent (Schoch-Bodmer). This is also the case in tracheids which show obvious signs of tip growth in their bifurcated and otherwise distorted ends (Wardrop and Dadswell 1951). Thus, in general, distribution of pits and tracheids and fibres is consistent with the assumption that the primary pit fields are regions of growth. A point to be taken into account, however, is the different function of tracheids and fibres in the stem which may be related to the terminal distribution of pits in tracheids. A further point of interest in this connection is the reported absence or decreased number of crassulae near the cell tips (Bannan and Whalley 1950). If these are regarded as the edges of primary pit fields formed by the crowding together of microfibrils (Plate 7, Fig. 1), then this process would be expected to be less apparent in areas of free extension at the ends of cells than would be the case near the middle of the cells where readjustment is more restricted.

It will also be apparent, on the considerations advanced above, that the regions of plasmodesmata and primary pit fields must be areas of cellulose synthesis. It may be significant therefore that, around these regions, secondary cell wall thickening begins (see, for example, Sachs. 1882). Examples of this can be seen in Plates 8 and 9, showing the secondary thickening surrounding pits in a vessel and fibre of *Ulmus* respectively. It may be noted that thickening appears to occur progressively around the pit fields, suggesting a directed synthesis of cellulose microfibrils (Wardrop and Dadswell 1951).

In this connection it is also of significance that the tips of mature tracheids often show considerable thickening, although a minute terminal canal exists between the lumen and primary wall (Wardrop and Dadswell 1952). It is suggested that this thickening arises when extension is complete, as it is known to be absent in partly mature cells. Furthermore, the observations of Gorter (1949) on the influence of 2,3,5-triiodobenzoic acid on the growth of root hairs demonstrate the synthetic activity of the cell tip during growth. All these considerations suggest that the cell tips, plasmodesmata, and primary pit fields are to be regarded as functionally similar. In this connection, it is interesting that tracheids from macerated xylem of *Pinus pinaster* may occasionally be found in which contact is made through the tip of one to a pit of another.

The scheme proposed in Figure 1 also receives some support from physiological data. Thus it can be seen that, in the expansion of the cell, synthesis of both cytoplasmic and cell wall substance is involved. However, the work of Bonner (1934) on the extension of coleoptile segments has shown that at 2°C extension may take place without the formation of cell wall material, whereas at 25°C both extension growth and cell wall formation take place, so that cell extension and cell wall formation are independent processes. This is in agreement with the later experiments of Gorter (1949), already referred to, in which cell wall formation took place, although cell extension was suppressed. However, the fact that extension can occur at 2°C without wall formation indicates there is some purely physical factor involved in growth. This is in agreement with the writer's (unpublished) data that the temperature coefficient of extension of coleoptile segments between 4° and 15°C is 1.1, and 1.9 between 15° and 24°C. Furthermore, on plasmolysis, the segments grown between 25° and 15°C contracted 6.9 per cent. and 7.1 per cent. respectively, whereas those grown at 4°C contracted 12.2 per cent. of the final length. In terms of the scheme in Figure 1, this might be taken to imply that the initial cytoplasmic expansion may involve only a physical change at low temperature, and the extension then taking place is not consolidated by the formation of cellulose microfibrils, whereas, at the higher temperatures, protein and cellulose syntheses are involved, which not only results in increased growth of the cell, but of the consolidation of the growth by formation of additional framework material which is reflected in the decreased contraction on plasmolysis.

It is apparent that, in a further analysis of the physical mechanism of growth, consideration must be given to the state of the protoplast, since any change in the protoplast involves changes in the physical state of the cell wall and is probably involved in tip growth in which the protoplast apparently extends through the loosened microfibrillar network. This may involve a localized change in protoplasmic viscosity (Northen 1940) or of permeability of the protoplast. In relation to this, it is of interest to recall the early experiments of Macallum (1929) on the distribution of potassium in plant cells, in which it was shown that these ions are concentrated in the regions of greatest extension growth, and it may be significant that potassium is known to decrease protoplasmic viscosity and increase the permeability of the protoplast to water (Höber 1946). Admittedly, Macallum's methods are open to objection, but the study of the distribution of potassium by improved methods may give some lead to the mechanism by which the changes in protoplasmic texture involved in extension growth take place. It is also clear that agents affecting growth in cells, such as auxins, must act primarily on the protoplast, as suggested earlier (see, for example, Audas 1949), rather than on the cell wall.

IV. ACKNOWLEDGMENTS

The author is indebted to his colleagues, Dr. H. E. Dadswell and Dr. I. V. Newman, for helpful discussion during the course of this work.

.V. REFERENCES

AUDAS, L. J. (1949).—*Biol. Rev.* 24 (1): 51.

BAILEY, I. W. (1920).—*Amer. J. Bot.* 7: 355.

BANNAN, M. W. (1950).—*Amer. J. Bot.* 37 (7): 511.

BANNAN, M. W., and WHALLEY, B. E. (1950).—*Canad. J. Res.* C 28: 341.

BONNER, J. (1934).—*Proc. Nat. Acad. Sci., Wash.* 20: 393.

BOSSHARD, H. H. (1952).—*Ber. schweiz. bot. Ges.* 62: 482.

CRAFTS, A. S. (1933).—*Plant Physiol.* 8: 81.

EAMES, A. J., and MACDANIELS, L. H. (1947).—"Introduction to Plant Anatomy." 2nd Ed. (McGraw-Hill: New York.)

FREY-WYSSLING, A. (1936).—*Protoplasma* 25: 261.

FREY-WYSSLING, A. (1952).—*Symp. Soc. Exp. Biol.* No. 6: 321.

FREY-WYSSLING, A., and STECHER, H. (1951).—*Experientia* 7: 420.

GORTER, C. J. (1949).—*Proc. Acad. Sci. Amst.* 52 (10): 1185.

HOBER, R. (1946).—"Physical Chemistry of Cells and Tissues." (Blakiston Co.: Philadelphia.)

HODGE, A. J., and WARDROP, A. B. (1950).—*Aust. J. Sci. Res.* B 3 (3): 265.
ITERSEN, G. VAN (1935).—Proc. Sixth Int. Bot. Congress, Amsterdam.
KERR, T., and BAILEY, I. W. (1934).—*J. Arnold. Abor.* 15: 327.
MACALLUM, A. B. (1929).—*Proc. Roy. Soc.* B 54: 440.
MEEUSE, A. D. J. (1941*a*).—*Rec. Trav. Bot. Néerl.* 38: 20.
MEEUSE, A. D. J. (1941*b*).—*Bot. Rev.* 7: 249.
MUHLETHALER, K. (1950).—*Ber. schweiz. bot. Ges.* 60: 614.
NEEFF, F. (1914).—*Z. Bot.* 6: 465.
NORTHEN, H. J. (1940).—*Biodynamica* 3: 10.
PRESTON, R. D., and WARDROP, A. B. (1949).—*Biochim. Biophys. Acta.* 3: 549.
PRIESTLEY, J. H. (1930).—*New Phytol.* 29 (2): 96.
PRIESTLEY, J. H., SCOTT, L. I., and MALINS, M. (1933).—*Proc. Leeds Phil. Lit. Soc.* 2: 365.
SACHS, J. (1878).—*Arb. Bot. Inst. Wurz.* 2 (1): 46.
SACHS, J. (1879).—*Arb. Bot. Inst. Wurz.* 2 (2): 185.
SACHS, J. (1882).—"Textbook of Botany." (Oxford.)
SCHOCH-BODMER, H., and HUBER, P. (1952).—*Proc. Leeds Phil. Lit. Soc.* 6 (1): 25.
SINNOTT, E. W., and BLOCH, R. (1939).—*Amer. J. Bot.* 26 (8): 625.
SINNOTT, E. W., and BLOCH, R. (1945).—*Amer. J. Bot.* 32: 151.
STECHER, H. (1952).—*Mikroskopie* 7: 30.
WARDROP, A. B., and DADSWELL, H. E. (1951).—*Nature* 168: 610.
WARDROP, A. B., and DADSWELL, H. E. (1952).—*Aust. J. Sci. Res.* B 5 (4): 385.

EXPLANATION OF PLATES 1-9

The electron micrographs in Plates 1-9 were photographed at an initial magnification of 3000. All specimens illustrated were shadowed with uranium at an angle of 8°.

PLATE 1

Pinus radiata. Part of a single wall from near the middle of a cell taken from the cambium zone. Cell axis vertical. × 16,000.

PLATE 2

Fig. 1.—*Pinus radiata.* As Plate 1 but near the tip of a differentiating tracheid undergoing bifurcation. Cell axis vertical. × 18,000.

Fig. 2.—As Plate 1 showing thin areas of a differentiating tracheid. Cell axis vertical. × 18,000.

PLATE 3

Eucalyptus elaeophora. Part of a single wall of a differentiating fibre taken from the cambium zone showing thin areas. Cell axis vertical. × 15,000.

PLATE 4

Eucalyptus elaeophora. The tip of a differentiating fibre taken from the cambium zone. Cell axis vertical. × 15,700.

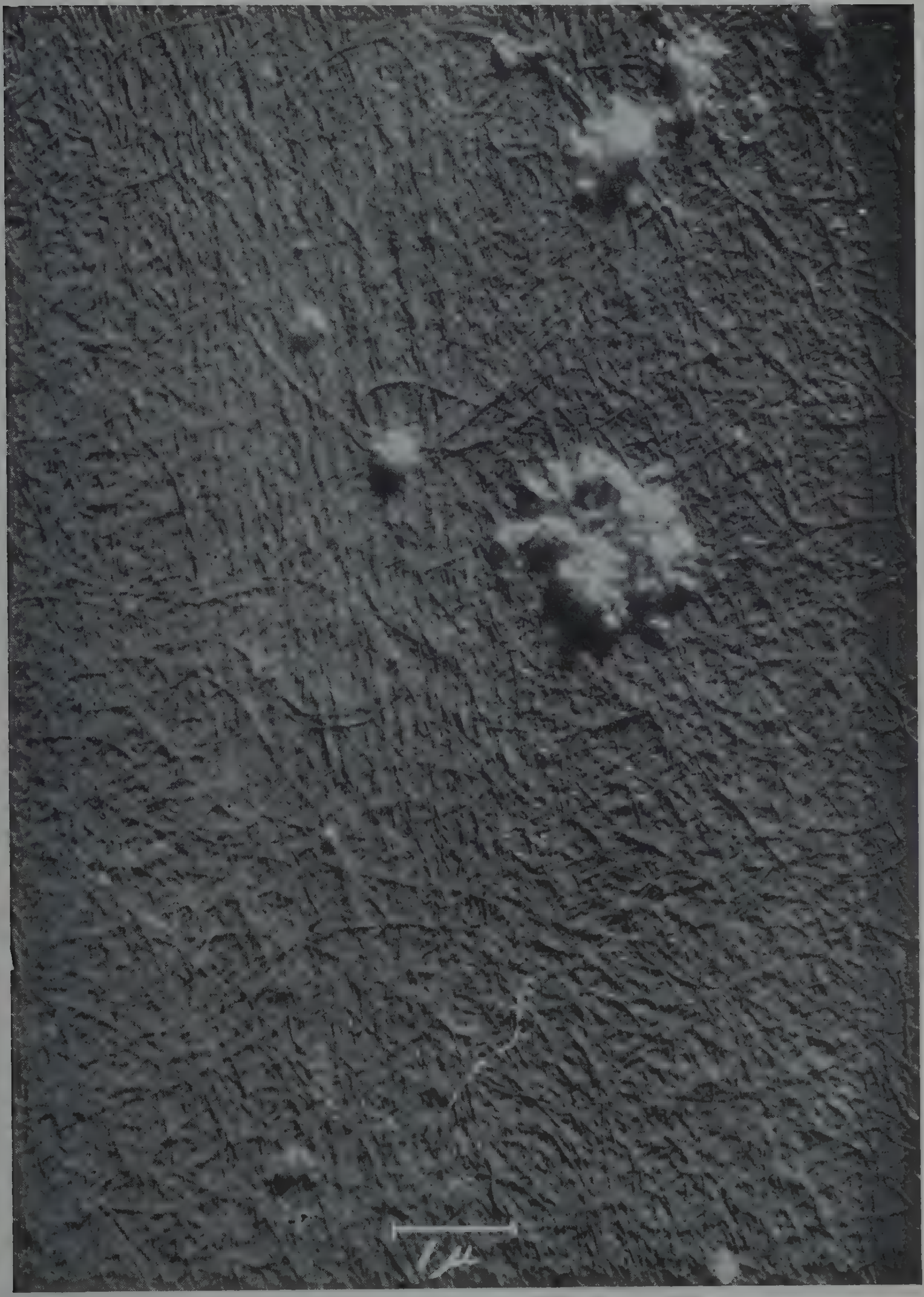
PLATE 5

Solanum tuberosum. Part of a cell wall from storage parenchyma showing areas of plasmodesmata. × 18,000.

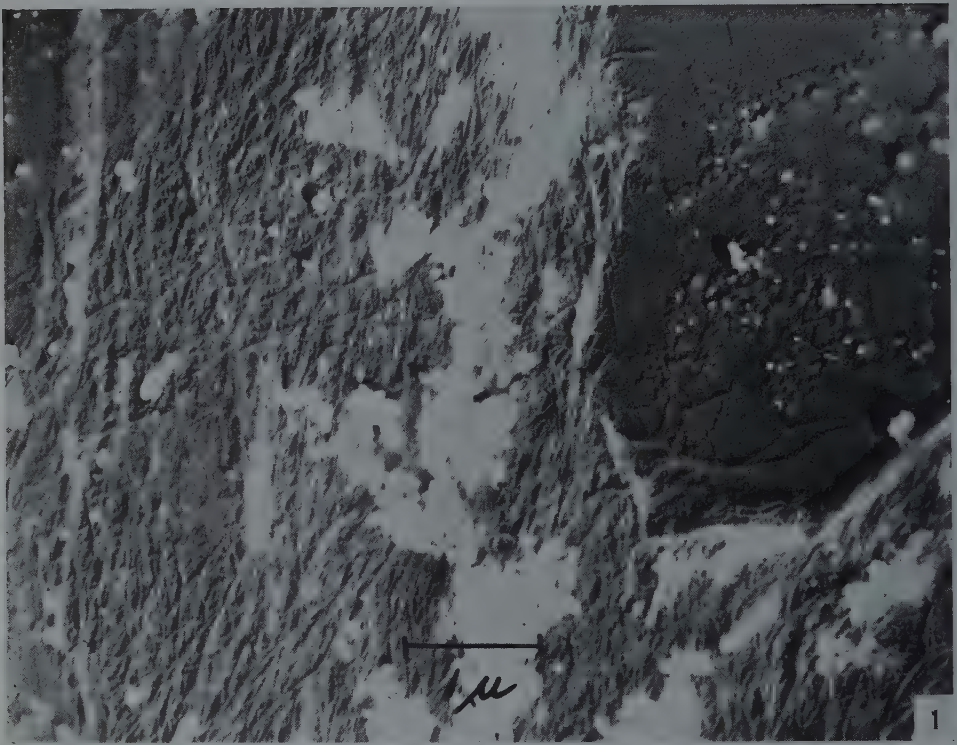
PLATE 6

As Plate 5, showing primary pit fields regarded as areas of enlarged and divided plasmodesmata. × 18,000.

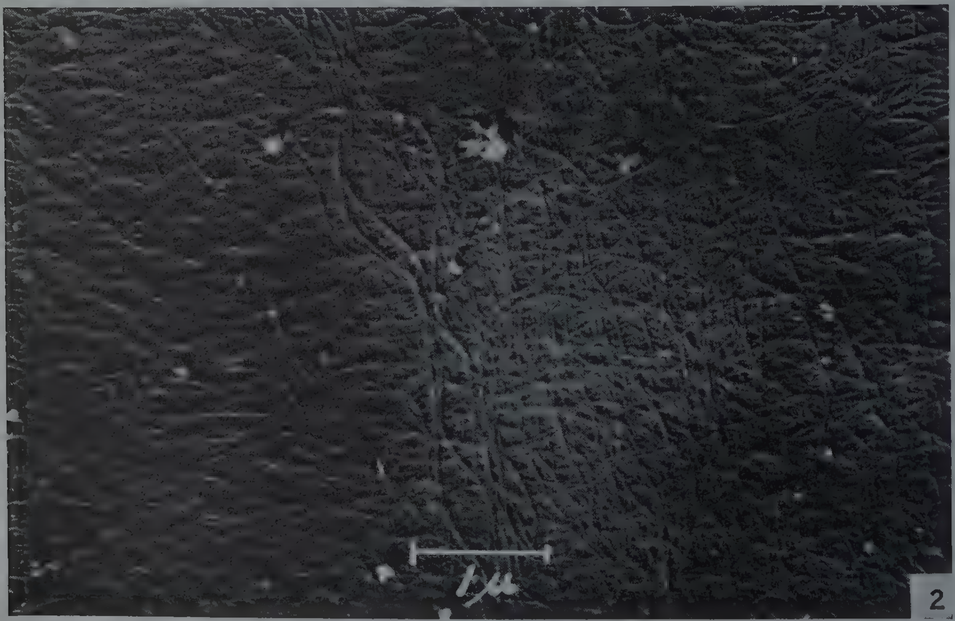
SURFACE GROWTH IN FIBRES AND TRACHEIDS



SURFACE GROWTH IN FIBRES AND TRACHEIDS



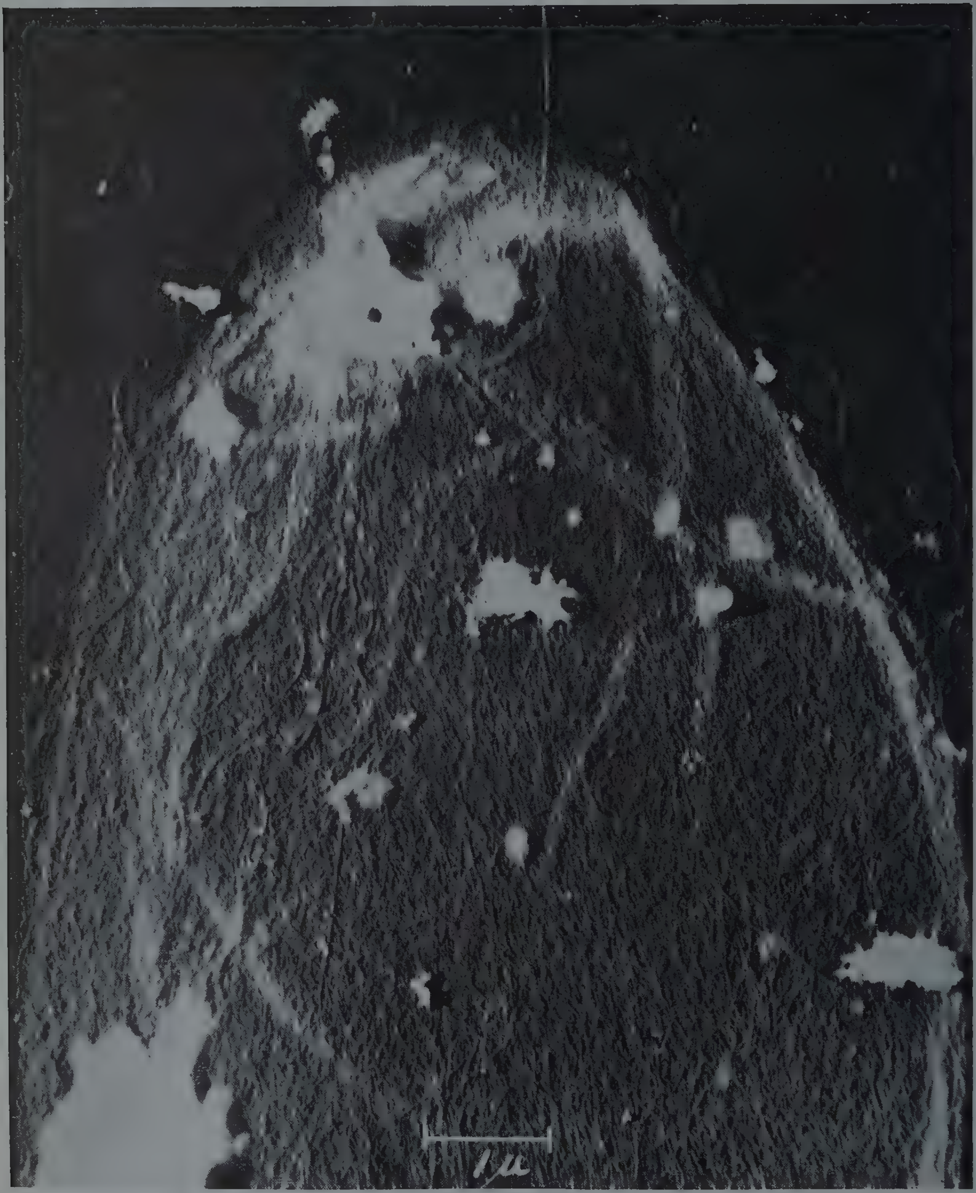
1

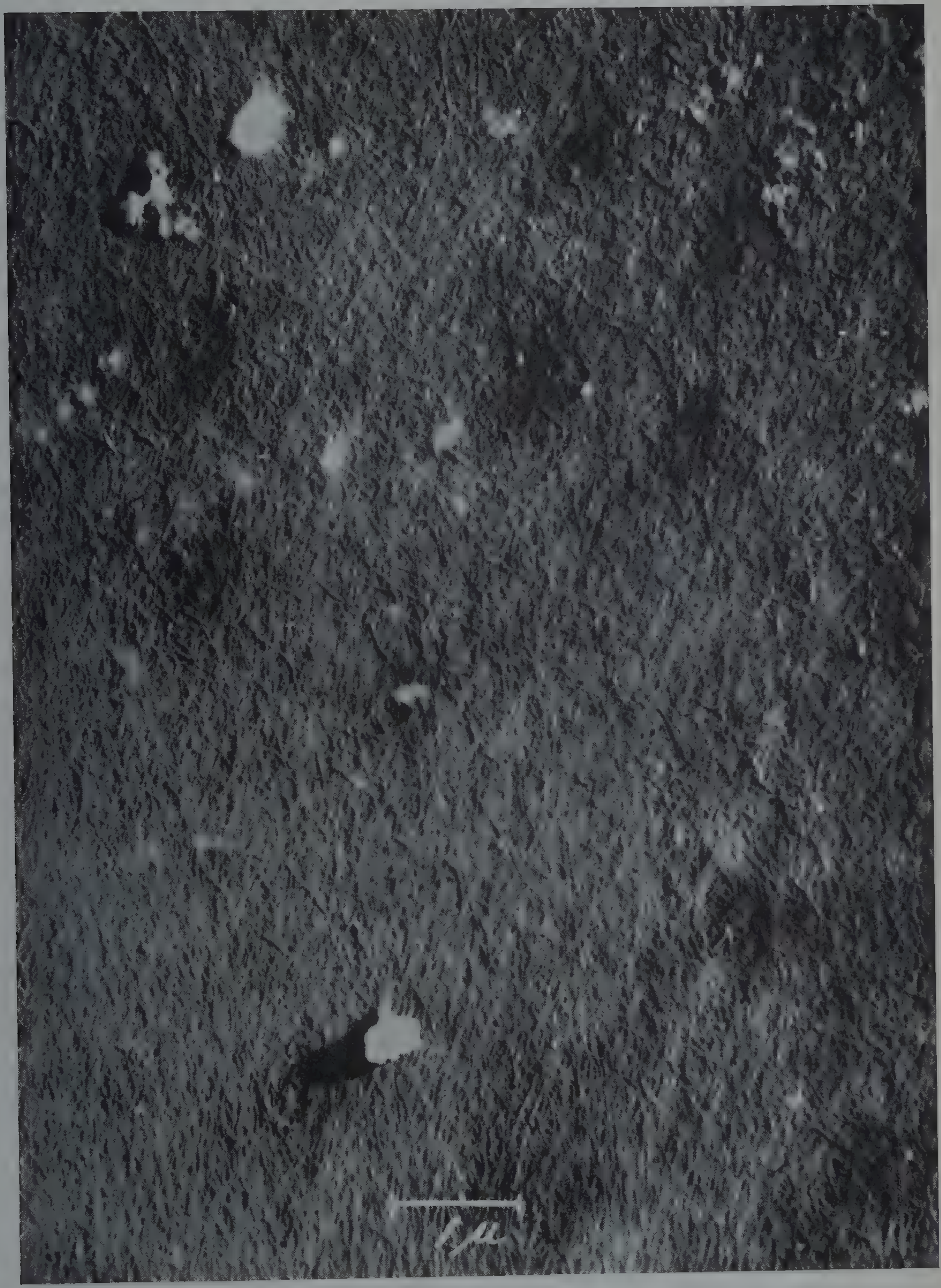


2

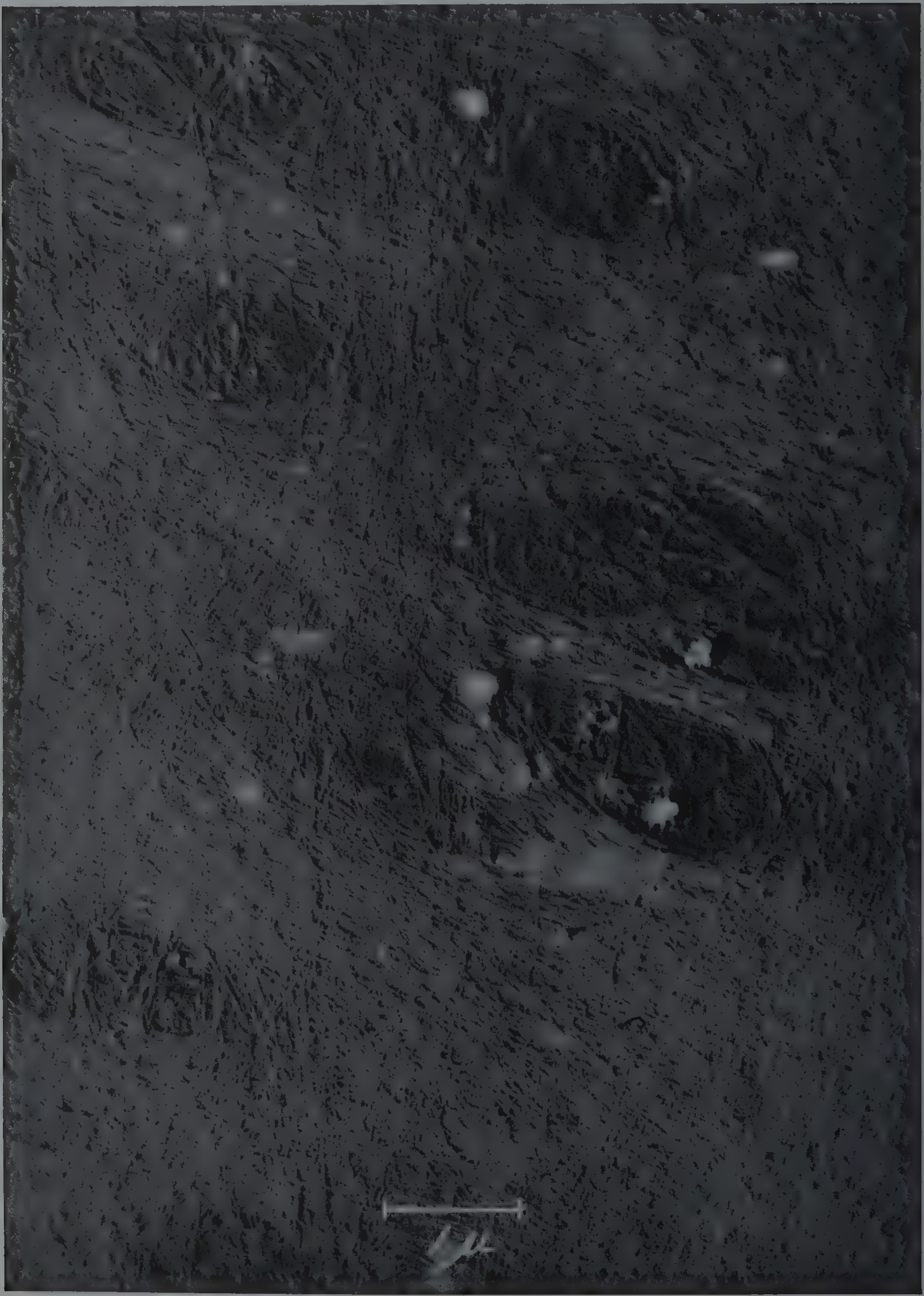
SURFACE GROWTH IN FIBRES AND TRACHEIDS

SURFACE GROWTH IN FIBRES AND TRACHEIDS

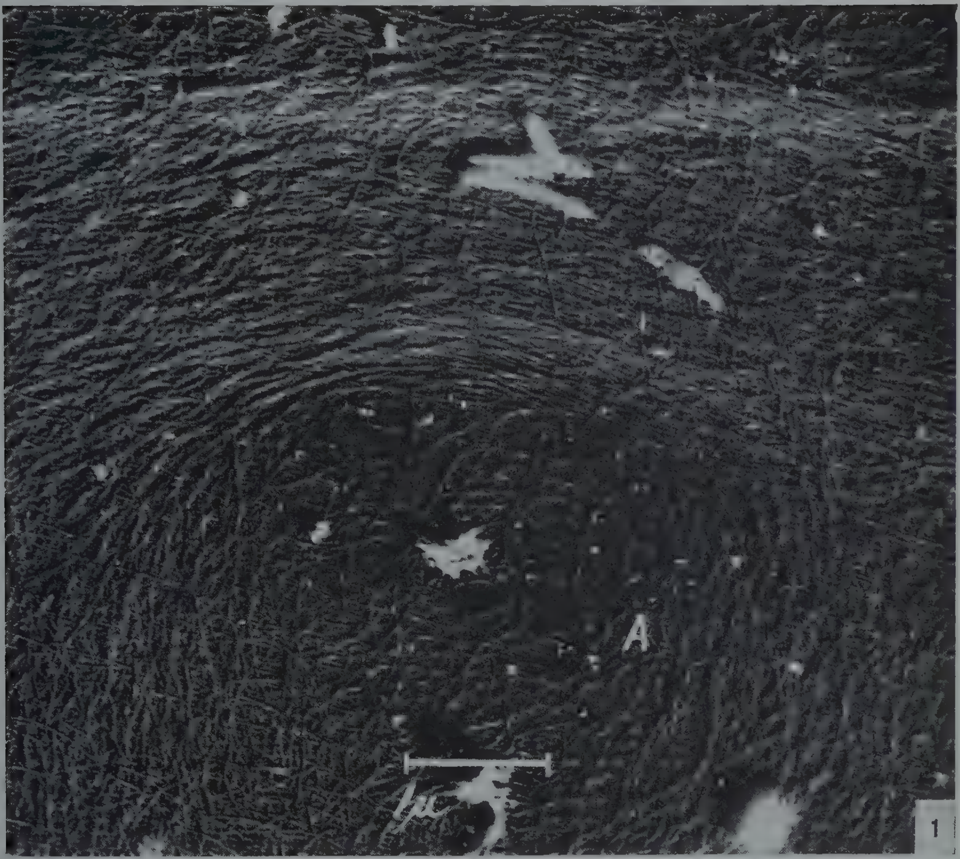


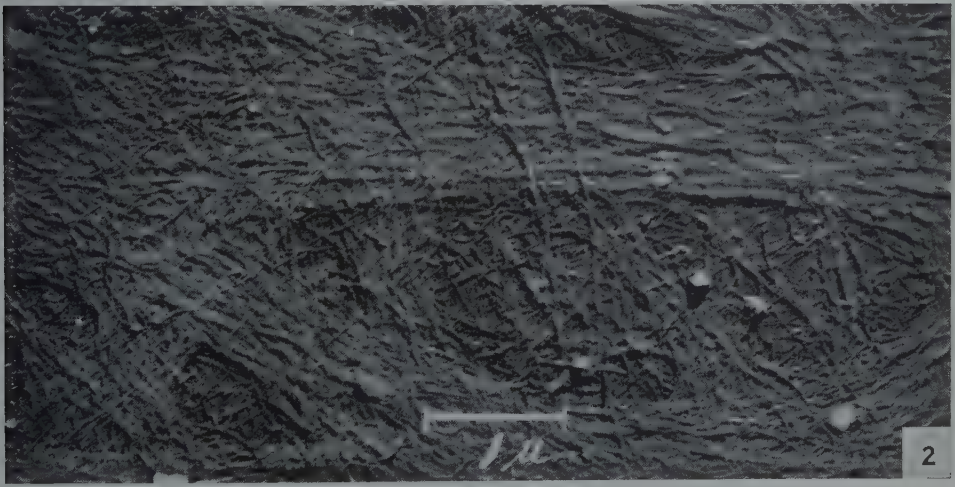

1 μ

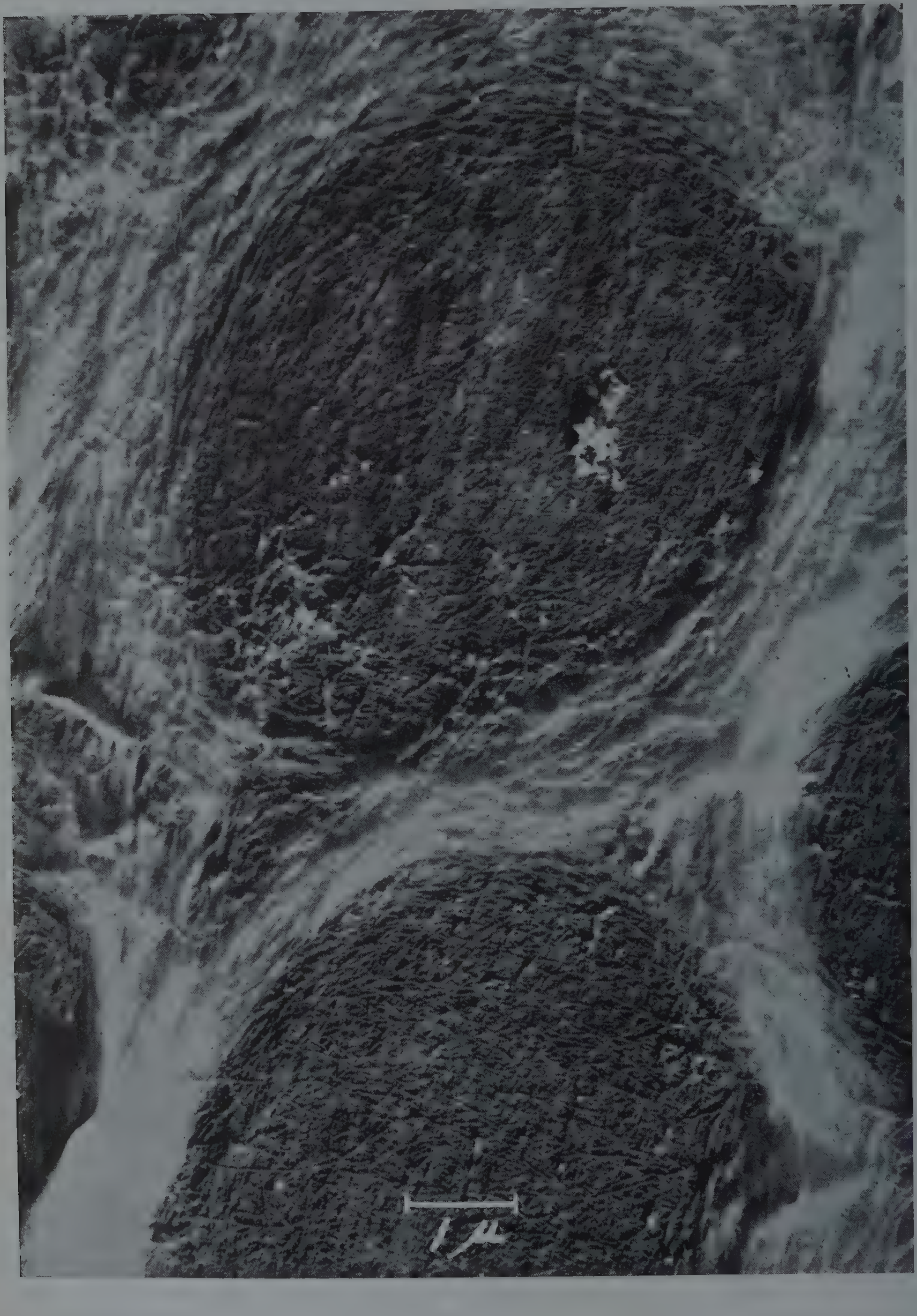
SURFACE GROWTH IN FIBRES AND TRACHEIDS



SURFACE GROWTH IN FIBRES AND TRACHEIDS






1 μ

SURFACE GROWTH IN FIBRES AND TRACHEIDS

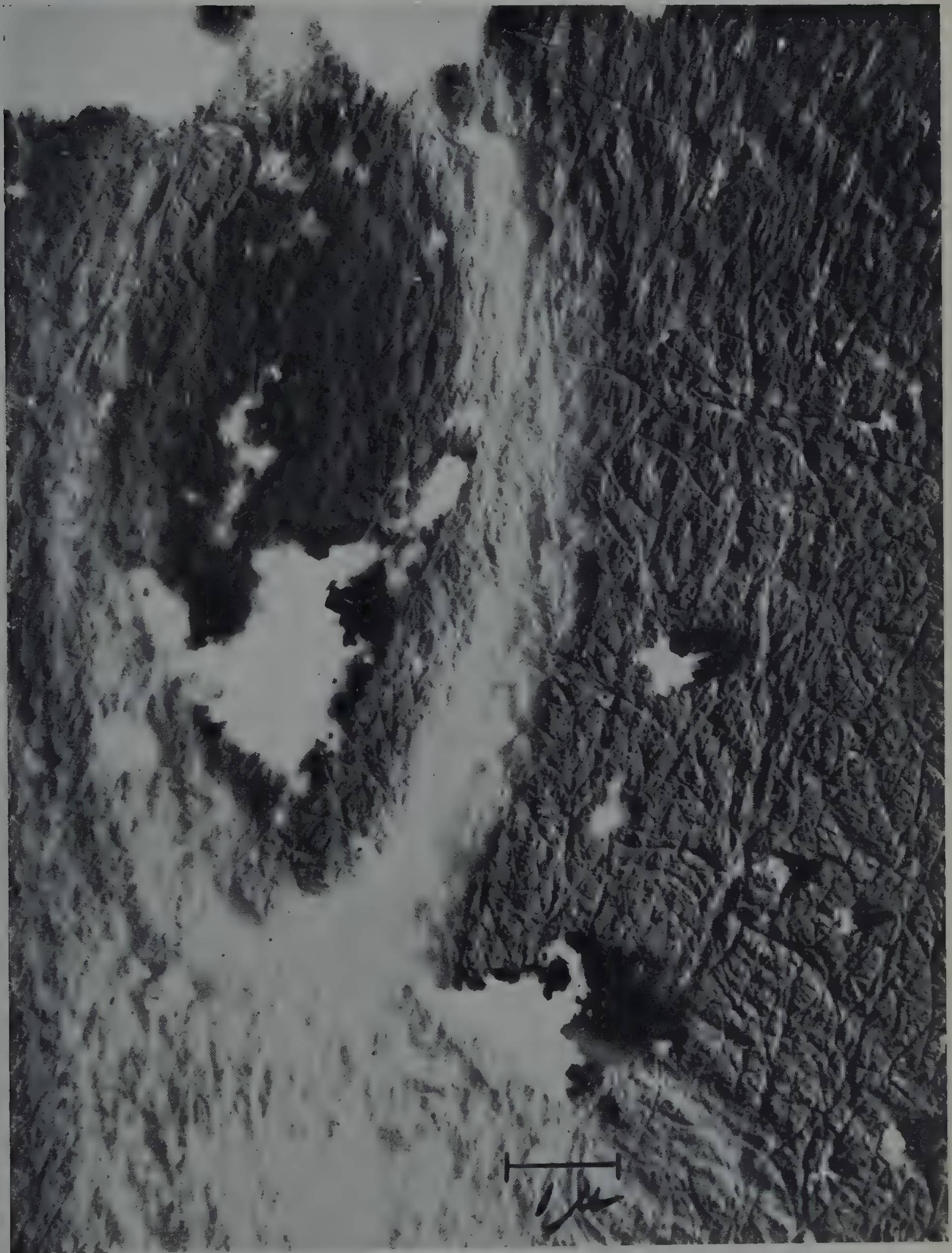


PLATE 7

Fig. 1.—*Pinus radiata.* Part of a differentiating tracheid from the cambium zone showing a thin area and a supposed crassula. Cell axis vertical. × 18,000.

Fig. 2.—*Solanum tuberosum.* Part of a cell wall from storage parenchyma showing primary pit fields. × 15,000.

PLATE 8

Ulmus sp. Part of the cell wall of a differentiating vessel taken from the cambium zone showing the commencement of secondary thickening. Cell axis horizontal. × 15,000.

PLATE 9

Ulmus sp. Part of the cell wall of a differentiating fibre taken from the cambium zone. Cell axis vertical. × 15,000.

ALUMINIUM ACCUMULATION IN THE AUSTRALIAN-NEW GUINEA FLORA

By L. J. WEBB*

(*Manuscript received September* 25, 1953)

Summary

Eighty aluminium-accumulating species were detected among 1324 species tested from the Australian-New Guinea flora. Accumulation was most strongly developed in certain dicotyledons (69 spp.) and Filicales (11 spp.).

A high aluminium content of the organs of accumulating plants appears to be associated with normal metabolism.

Recorded accumulators are mainly restricted to what are usually regarded as the more primitive groups in dicotyledons and Filicales, suggesting that accumulation is a physiological relic in these groups.

Obligate accumulators are confined to leached acid soils from a variety of parent materials, in comparatively high-rainfall areas.

The re-deposition of aluminium in vegetable debris beneath Australian rain-forest communities dominated by accumulators (e.g. *Ceratopetalum apetalum* D. Don.) may be an important ecological and pedogenic factor.

The significance of accumulation is discussed along biochemical, ecological, and taxonomic lines.

There is evidence that accumulation is an adjunct of specialization (i.e. relatively narrow physiological tolerances), chiefly among tree species able to exploit impoverished soils in relatively primitive, generally tropical, mesic habitats.

Accumulation seems a useful special character to supplement other data in the clarification of some taxonomic problems.

I. INTRODUCTION

In the course of an Australian phytochemical survey begun in 1945, aluminium succinate was found as a massive deposit in a cavity (a so-called "wind shake") in the heartwood of *Cardwellia sublimis* F. Muell. (Proteaceae). Analyses showed that this tree accumulates considerable quantities of aluminium in bark, wood, and leaves (Webb 1952). A similar occurrence of basic aluminium succinate, of suggested constitution $Al_2(C_4H_4O_4)_3Al_2O_3$, had been reported in *Orites excelsa* R.Br., also of the family Proteaceae (Maiden and Smith 1895; Smith 1903). Smith supposed that the deposit was excretory in function, and "probably nature's method for getting rid of an excess" of aluminium. Basic aluminium succinate was also found as a hard white deposit in galleries of the larva of a longhorn beetle in wood of *Qualia* sp. (Vochysiaceae), but Smith's formula was considered doubtfully valid (Campbell, Packman, and Rolfe 1945). The deposit was thought to have originated by a flow into the cavities of sap containing suitable proportions of aluminium and succinic acid, followed by evaporation of water. In a recent review, Hutchinson (1943) listed various "aluminium-accumulators", and discussed physiological and ecological aspects of accumulation in plants and other organisms. It has been assumed that the element is required for normal growth of gross aluminium accumulators. Reference has also been made (Hutchinson 1943; Chenery 1948*a*, 1949) to the possible taxonomic significance of accumulation. Accumulation is used here in the sense defined by Robinson and Edgington (1945), when "Certain plants take up the particular element in quantities very far above, sometimes many thousand times above, the average quantity for 'normal' plants".

---

* Division of Plant Industry, C.S.I.R.O., Brisbane.

II. Materials and Methods

The "aluminon" test for aluminium described by Chenery (1948*a*) was used. This method permits the assessment, by intensity of colour, of several levels of aluminium content ranging from about 300 to over 10,000 p.p.m. Chenery (1949) has shown the qualitative results to be well supported by quantitative analyses, and regards a content of 1,000 p.p.m. or greater as necessary to qualify a plant as an accumulator. In the following results, colours with the aluminon reagent which suggested a level < 1000 p.p.m. were regarded as negative tests.

In many cases, bark as well as leaves was tested. Herbarium specimens collected during the phytochemical survey were generally accompanied by bark samples. In addition, leaf specimens from the Queensland Herbarium were tested, and provide a general coverage of the flora of Queensland, but only a limited coverage for other States. About 300 New Guinea specimens (mainly rain-forest) were included. Most attention was paid to dicotyledons and Filicales, and plants of rain-forests were more thoroughly sampled than those of other communities.

III. Results

A total of 1324 species was tested. For convenience of reference, the families are arranged in alphabetical order.

SPERMATOPHYTA—Dicotyledons (Total 69/1154*).

Acanthaceae 0/2; Aizoaceae 0/2; Akaniaceae 0/1; Alangiaceae 0/1; Amaranthaceae 0/2; Ampelidaceae 0/2; Anacardiaceae 0/4; Annonaceae 0/5; Apocynaceae 0/26; Aquifoliaceae 0/2; Araliaceae 0/5; Aristolochiaceae 0/3; Asclepiadaceae 0/13; Bignoniaceae 0/3; Boraginaceae 0/10; Burseraceae 0/3; Campanulaceae 0/1; Capparidaceae 0/7; Caprifoliaceae 0/1; Caryophyllaceae 0/1; Casuarinaceae 0/2; Celastraceae 0/11; Cephalotaceae 0/1; Chenopodiaceae 0/4; Chloranthaceae 0/1; Cochlospermaceae 0/1; Combretaceae 0/6; Compositae 0/20; Connaraceae 0/1; Convolvulaceae 0/4;

---

* The numerator refers to the number of accumulating species, and the denominator to the total species tested. When a family is positive, the genera are also listed in alphabetical order, and the positive genera and families are printed in bold type.

Cruciferae 0/5; Cucurbitaceae 0/6; **Cunoniaceae** 10/28: *Ackama* 0/2, ***Anodopetalum*** 1/1; *Aphanopetalum* 0/1, *Bauera* 0/3, *Callicoma* 0/1, ***Ceratopetalum*** 5/5, *Davidsonia* 0/1, *Geissois* 0/2, ***Gillbeea*** 1/1, *Opocunonia* 0/2, *Pseudoweinmannia* 0/4, *Pullea* 0/1, ***Schizomeria*** 2/2, *Spiracanthemum* 0/1, ***Stollaea?*** 1/1; Datiscaceae 0/1; Dilleniaceae 0/6; Dipterocarpaceae 0/2; Droseraceae 0/1; Ebenaceae 0/8; Elaeagnaceae 0/1; Epacridaceae 0/4; Ericaceae 0/2; Erythroxylaceae 0/2; **Escalloniaceae** 7/18: *Abrophyllum* 0/1, *Argophyllum* 0/4, *Anopterus* 0/2, *Colmeiroa* 0/1, *Cuttsia* 0/1, ***Polyosma*** 5/5, ***Quintinia*** 2/4; **Euphorbiaceae** 3/56: *Acalypha* 0/2, *Actephila* 0/1, *Adriana* 0/1, ***Antidesma*** 1/1, ***Aporosa*** 1/1, ***Baccaurea*** 1/1, *Baloghia* 0/1, *Beyeria* 0/1, *Breynia* 0/4, *Bridelia* 0/1, *Claoxylon* 0/1, *Cleistanthus* 0/1, *Codiaeum* 0/1, *Coelebogyne* 0/2, *Croton* 0/4, *Dissiliaria* 0/1, *Euphorbia* 0/4, *Excoecaria* 0/2, *Fontainea* 0/1, *Glochidion* 0/4, *Hemicyclia* 0/2, *Homalanthus* 0/1, *Macaranga* 0/4, *Mallotus* 0/8, *Petalostigma* 0/3, *Phyllanthus* 0/1, *Pimeleodendron* 0/1, *Securinega* 0/1; Eupomatiaceae 0/1; Fagaceae 0/4; Flacourtiaceae 0/8; Geraniaceae 0/2; Gesneriaceae 0/1; Goodeniaceae 0/2; Guttiferae 0/7; Hamamelidaceae 0/1; Hernandiaceae 0/3; Himantandraceae 0/2; Hippocrateaceae 0/1; Icacinaceae 0/10; Juglandaceae 0/1; Labiatae 0/3; Lauraceae 0/36; Lecythidaceae 0/5; Leguminosae 0/84; Lobeliaceae 0/2; Loganiaceae 0/11; Loranthaceae 0/6; Magnoliaceae 0/2; Malpighiaceae 0/1; Malvaceae 0/8; **Melastomaceae** 3/3: ***Astronia*** 2/2, ***Melastoma*** 1/1; Meliaceae 0/25; Menispermaceae 0/9; **Monimiaceae** 7/27: *Atherosperma* 0/1, *Daphnandra* 0/5, *Doryphora* 0/1, *Dryadodaphne* 0/1, ***Hedycarya*** 1/3, *Levieria* 0/1, *Matthaea* 0/1, *Palmeria* 0/1, *Piptocalyx* 0/1, *Steganthera* 0/1, ***Tetrasynandra*** 1/3, *Trimenia* 0/1, ***Wilkiea*** 4/5; Moraceae 0/11; Myoporaceae 0/6; Myristicaceae 0/4; Myrsinaceae 0/8; Myrtaceae 0/66; Nyctaginaceae 0/1; Ochnaceae 0/1; Olacaceae 0/1; Oleaceae 0/9; Onagraceae 0/1; Oxalidaceae 0/2; Passifloraceae 0/3; Phytolaccaceae 0/3; Piperaceae 0/6; Pittosporaceae 0/10; Plantaginaceae 0/1; Plumbaginaceae 0/1; Polygalaceae 0/16; Polygonaceae 0/2; **Proteaceae** 20/74: *Adenanthos* 0/1, ***Austromuellera*** 1/1, ***Banksia*** 1/6, *Buckinghamia* 0/1, ***Cardwellia*** 1/1, *Carnarvonia* 0/1, *Conospermum* 0/1, *Darlingia* 0/1, *Dryandra* 0/1, *Embothrium* 0/2, *Finschia* 0/1, *Grevillea* 0/15, *Hakea* 0/3, ***Helicia*** 9/10, ***Hicksbeachia*** 1/1, *Isopogon* 0/1, ***Kermadecia*** 1/1, *Lomatia* 0/5, *Macadamia* 0/4, ***Orites*** 3/3, *Persoonia* 0/3, *Petrophila* 0/1, ***Placospermum*** 1/1, *Stenocarpus* 0/2, *Strangea* 0/1, *Synaphea* 0/1, *Telopea* 0/2, ***Xylomelum*** 2/3; Ranunculaceae 0/1; Rhamnaceae 0/12; Rhizophoraceae 0/2; Rosaceae 0/3; **Rubiaceae** 8/128: *Abbottia* 0/1, *Anthocephalus* 0/1, *Antirhea* 0/2, *Asperula* 0/7, *Borreria* 0/3, *Canthium* 0/9, ***Coelospermum*** 1/2, *Coprosma* 0/6, *Dentella* 0/1, *Diplospora* 0/3, *Galium* 0/4, *Gardenia* 0/8, *Geophila* 0/1, *Guettarda* 0/1, ***Hedyotis*** 1/4, *Hodgkinsonia* 0/2, *Hydnophytum* 0/1, *Ixora* 0/6, *Knoxia* 0/1, ***Lasianthus*** 1/2, *Mastixiodendron* 0/1. ***Morinda*** 1/5, *Mussaenda* 0/2, *Myrmecodia* 0/1, *Nauclea* 0/1, *Neonauclea* 0/2, ***Oldenlandia*** 1/5, *Opercularia* 0/4, *Ophiorrhiza* 0/1, *Pavetta* 0/4, *Pomax* 0/1, ***Psychotria*** 3/11, *Randia* 0/12, *Richardia* 0/2, *Scyphiphora* 0/1, *Synaptantha* 0/1, *Tarenna* 0/1, *Timonius* 0/3, *Uncaria* 0/2, *Wendlandia* 0/3; Rutaceae 0/81; Santalaceae 0/2; Sapindaceae 0/40; Sapotaceae 0/12; Saurauiaceae 0/1; Simaroubaceae 0/4; Solanaceae 0/15; Sterculiaceae 0/9; Stylidiaceae 0/1; **Symplocaceae** 8/8: ***Symplocos*** 8/8; **Ternstroemiaceae** 2/3: ***Gordonia*** 1/1, ***Ternstroemia*** 1/2; Thymelaeaceae 0/5; Tiliaceae 0/8; Ulmaceae 0/2; Umbelliferae 0/5; Urticaceae 0/6; Vacciniaceae 0/3; Verbenaceae 0/24; Violaceae 0/1; Winteraceae 0/1.

Monocotyledons (Total 0/69)

Amaryllidaceae 0/2; Commelinaceae 0/2; Cyperaceae 0/14; Dioscoreaceae 0/2; Eriocaulaceae 0/1; Gramineae 0/16; Haemodoraceae 0/17; Liliaceae 0/5; Orchidaceae 0/1; Palmae 0/2; Pandanaceae 0/1; Philydraceae 0/1; Smilacaceae 0/1; Xyridaceae 0/4.

Gymnosperms (Total 0/14)

Coniferae 0/8; Cycadaceae 0/5; Gnetaceae 0/1.

PTERIDOPHYTA (Total 11/87)

Marattiales.—Marattiaceae 1/1: ***Angiopteris*** **1/1.**

Filicales.—Aspidiaceae 0/9; Aspleniaceae 0/4; Blechnaceae 0/2; **Cyatheaceae** 2/5: ***Cyathea*** 2/5; Davalliaceae 0/4; **Gleicheniaceae** 2/3: ***Dicranopteris*** 1/1, *Gleichenia* 0/1, ***Sticherus*** 2/2; **Hymenophyllaceae** 1/14: *Cephalomanes* 0/1, *Crepidomanes* 0/1, *Crepidopteris* 0/1, *Gonocormus* 0/1, *Hemicyatheon* 0/1, *Hymenophyllum* 0/1, *Macroglena* 0/1, *Mecodium* 0/2, *Microgonium* 0/1, *Pleuromanes* 0/1, *Polyphlebium* 0/1, ***Selenodesmium*** 1/1, *Vandenboschia* 0/1; Marsileaceae 0/1; Plagiogyriaceae 0/1; **Polypodiaceae** 1/9: ***Dipteris*** 1/1, *Drynaria* 0/1, *Platycerium* 0/3, *Polypodium* 0/2, *Pyrrosia* 0/2; **Pteridaceae** 2/23: *Acrostichum* 0/1, *Adiantum* 0/1, *Cheilanthes* 0/1, *Culcita* 0/1, *Dennstaedtia* 0/1, *Dicksonia* 0/2, *Histiopteris* 0/1, *Hypolepis* 0/2, ***Lindsaea*** 2/9, *Pellaea* 0/1, *Pteridium* 0/1, *Pteris* 0/2; Schizaeaceae 0/3.

Lycopodiales.—Lycopodiaceae 1/7: ***Lycopodium*** **1/7.**

In several cases, variations in results occurred when samples of the same species were tested from different localities, or when different parts of the tree were tested. These were:

Psychotria coelospermum F. M. Bail. (Rubiaceae), positive from one, and negative from five localities. The positive sample was from a plant growing in a swamp.

Helicia diversifolia C. T. White (Proteaceae), positive from five, negative from five localities. Two specimens from the same place gave different results. One of these negative samples was noted as from "young growth".

H. glabrescens C. T. White (Proteaceae), positive from nine, negative from one locality close to the other areas.

Xylomelum scottianum F. Muell. (Proteaceae), positive from seven, negative from one locality.

Quintinia sieberi A. DC. (Escalloniaceae), positive from two localities, negative from seven localities. This plant establishes itself as an epiphyte on tree-ferns, and its roots later reach the ground. Two of the negative samples were noted as from small trees on tree-ferns. The closely related *Q. verdonii* F. Muell. was uniformly positive from seven localities. It does not generally begin life on tree-ferns.

Melastoma polyanthum Blume (Melastomaceae), positive from 12 localities, negative from one locality.

In the above examples, except where otherwise noted, it was not possible to discover from the herbarium labels or field notes any differences in habitat or size which would account for the differences in aluminium content. In all cases, tests were repeated with concordant results.

Ervatamia punctulata (Wbg.) Mgf., *Voacanga papuana* (F. Muell.) K. Schum (Apocynaceae), and *Stollaea* sp.? (Cunoniaceae) bark was positive, leaf negative.

Aporosa sp. (Euphorbiaceae) leaf was positive, bark negative.

These variations suggest that aluminium accumulation is not always obligatory among individuals of some species.

IV. Discussion of Results

While the immediate aim of taxonomy is often an expedient one, to permit the convenient classification of plants, a further aim attempts to reveal something of their phylogenetic relationships. For this purpose in particular, the many new facts disclosed by genetical, ecological, and biochemical studies may be added to the morphological criteria upon which conventional systems of classification are built. Comparative biochemistry has as yet contributed little to the new systematics of plants. Available chemical data exist as by-products of research into therapeutic or other economic compounds, or because the plant in question has yielded crystallizable substances attractive to the structural chemist. There has not yet been any general attempt to provide chemical data for plant taxonomists. Nevertheless, systematic chemical surveys of various families for alkaloids, saponins, coumarins, and pigments are beginning to piece together a useful chemical picture for restricted groups. Thus much information is being gathered in the phytochemical survey of the alkaloids and coumarins of Australian Rutaceae. It must be admitted that special characters, whether cytogenetical, chemical, or morphological, are of only limited value in taxonomy. Chemical data based on wide series of different compounds are ultimately required. Aluminium accumulation alone, without additional information on other characteristic constituents of the plants, cannot provide a sovereign interpretation of relationships to displace systems based on general characters. Accumulation can nevertheless be used in a supplementary way to confirm or refute opinions and suggested solutions of taxonomic problems. In one case (Lycopodiaceae) data are available for alkaloids as well. The use of chemical information, mainly on alkaloids, to clarify several problems of classification in Australian Rutaceae (on specific and higher levels) will be presented in another paper.

Below, the biochemical role of aluminium in the accumulating plant, and the relation of accumulation to ecological conditions, will be discussed as a prelude to the attempted use of accumulation as a "tool" in the taxonomy of several local families.

(*a*) *Biochemical and Anatomical*

Although Hutchinson (1943) and Chenery (1948*a*, 1949) have compiled extensive lists of known aluminium accumulators, there is no satisfactory evidence available as to the form in which aluminium occurs in the majority of these plants. Exceptions are aluminium succinate in heartwood cavities of *Orites excelsa* and *Cardwellia sublimis*, and in galleries of a wood-boring insect in timber of *Qualia* sp. (Campbell, Packman, and Rolfe 1945), the Al-pigment complex in *Hydrangea* and a few other plants (Chenery 1948*b*), and probably aluminium oxalate in *Mouriria marshalli* Burtt-Davy & Sandw. and several other trees (Chenery 1946).

Hutchinson (1945) referred to the supposed identification of aluminium in cell inclusions of *Symplocos,* in the palisade tissue in the leaves of all species of which Metcalfe and Chalk (1950, p. 891) noted the occurrence of "fat-like bodies", sometimes termed alumina bodies.

There does not appear to be available any satisfactory micro-method for the identification of aluminium compounds *in situ* in plant tissues. The accompanying photomicrographs (× 225) of the wood of *Orites excelsa* and *Cardwellia sublimis* show characteristic inclusions (rounded black bodies) in the ray cells. Since these species are accumulators, and the deposits resemble in shape those regarded elsewhere as alumina bodies (Metcalfe and Chalk 1950, p. 891), it might be inferred that the present deposits contain aluminium, or even aluminium succinate. It was not found practicable to demonstrate this experimentally. Irrigation of wood sections of *Cardwellia sublimis* with aluminon reagent gave a deeper red colour in the ray parenchyma and vessels. In shavings of the wood (tangential section), small powdery white streaks (1-3 by 0.5-1 mm) are conspicuous in rays and vessels, and when isolated by a dissecting needle, gave strongly positive tests for aluminium.

About 32 other species of Australian trees contain microscopic globules in the wood (mostly in the ray cells) which are, in shape, reminiscent of those in *Cardwellia* and *Orites* (G. L. Amos, personal communication). Except for three members of Proteaceae, these species did not qualify as aluminium accumulators. Therefore, unless this has been demonstrated, it is probably best to regard similar inclusions as pseudo-aluminous.

The known occurrence of basic aluminium succinate in cavities in the heartwood of *Cardwellia, Orites,* and *Qualia* raises some interesting biochemical questions. The deposits, while rarely encountered, are apparently not pathological in origin (Smith 1903). Campbell, Packman, and Rolfe (1945) considered that aluminium succinate may be deposited in cavities formed in sapwood by any agency, and this led Chenery (1946) to drill holes in several Trinidad accumulating trees, but the results of this investigation have not yet been seen. Hutchinson (1943) suggested that aluminium is required for ordinary growth of *Symplocos* and other gross accumulators, and reviewed the evidence for the metabolic role of aluminium in normal plants. Much of the evidence is inadequate. Without further biochemical work, interpretations of aluminium accumulation are only speculative.

Although Chenery (1948) has noted bright blue fruits among dicotyledons as a possible diagnostic feature for an accumulator, a number of local species with fruits of this colour (e.g. *Elaeocarpus, Delarbrea*) gave negative tests.

Accumulation of certain elements by Australian plants may be of direct economic significance. Thus marine borer resistance of timber of

Australian turpentine (*Syncarpia laurifolia* Ten.) has been correlated with high silica content (Amos and Dadswell 1948; Amos 1952).

(*b*) *Ecological*

As would be expected, none of the local accumulators is found on alkaline soils. Most of them are inhabitants of mesic closed forest formations in eastern Australia, such as rain-forests. Specimens of the same species of accumulator were tested from various localities, and with several exceptions listed previously, gave uniformly positive results. This would indicate that the positive species are generally obligate accumulators. In all cases, the plants were restricted to leached acid soils derived from a variety of parent rocks, including granite, rhyolite, basalt, and various sedimentaries.

In no case were accumulators detected on the alkaline soils of the dry inland parts of the country, nor are the genera and groups characteristic of these regions recorded as accumulators in the extensive tests by Chenery (1948*a*, 1949). A large proportion of accumulators in tropical rain-forests was also found by Muir (1950). Stoklasa (quoted by Hutchinson 1943) did in fact conclude that aluminium content is uniformly low in both aerial and subterranean parts of xerophytes, whereas it is most marked in hygrophytic species. Inability to accumulate has accompanied the adaptation of certain groups (e.g. Proteaceae) to xeric conditions and less acid soils. The significance of this loss in the evolution of various families will be discussed in the following section on taxonomy.

The alumina content of certain plants has been reported to vary in a general way with the acidity of the soil, but the relation between the two factors is complex. Thus availability of calcium and organic matter are correlated with decrease and increase respectively of the alumina content of certain plants (Robinson and Edginton 1945). Higher alumina in leaves and twigs was found in oak trees growing in clay, compared with trees growing "in ordinary soil" (Keller 1949). The pH of cell sap of accumulators is low e.g. 4.3-4.8 (Chenery 1948*b*), and in acid soils containing aluminium phosphate, plants with a sufficiently acid cell sap would have a means of utilizing soluble phosphate. Aluminium tolerance may therefore be considered one advantageous physiological factor under such conditions, and may influence competition among different species (cf. Gilbert and Pember 1935).

The continuous fall of leaves, bark, and woody debris from accumulating trees undoubtedly affects the distribution of aluminium in the soil profile. The concentration of phosphorus, calcium, zinc, etc. ("biophils") in topsoils by certain plants is already known to be of agricultural importance (cf. Leeper 1952). Under natural conditions, concentrations of aluminium in the surface layers of the soil under accumulators may be an ecological factor in the ecesis of certain species.

These considerations are of significance for various plant communities in Australia, e.g. communities dominated by coachwood (*Ceratopetalum apetalum* D. Don.) in New South Wales. This tree is an accumulator, and is widely spread under suitable climatic conditions on yellow-red podsolics from rhyolite and shales of the Neranleigh-Fernvale series. Other accumulating tree species which are often dominant in coachwood communities are *Orites excelsa* R. Br. and *Schizomeria ovata* D. Don. It would seem that the aluminium returned to the soil by the leaf litter is rapidly absorbed by the coachwood trees, forming a closed cycle. In a profile examined at Whian Whian State Forest, near Lismore, N.S.W., there was leaf litter (A_{00} horizon) of 1-2 in. deep, and an A_0 horizon of approx. 9 in., containing many small roots, and which probably absorbs all rain, except the heaviest and most persistent showers. Analysis of intact leaves sampled in July 1952 (midwinter) from litter uncontaminated with soil gave an alumina content of 0.53 per cent. (dried). One sample of leaves from small living coachwood trees contained 1.1 per cent. alumina (dry weight basis).

It was calculated that the top layer of the leaf litter (less than 1 in. deep) carried about 10 lb of alumina per acre. This is equivalent to approx. 3 g alumina per sq. m. of litter 6 cm thick. For a similar volume of leaf litter under a Trinidad seasonal forest, Chenery (1951), calculated that 3.5 g of alumina would be deposited annually. In the Australian community, total leaf fall on an annual basis would increase several-fold the 3 g alumina found in the one sampling. Thus the return of aluminium to the topsoil under this Australian subtropical community (dominated by an accumulator) is several times that computed by Chenery for a Trinidad community. This considerably reduces the 700 yr calculated by Chenery (1951) as necessary to raise by 1 per cent. the alumina content of the top 10 cm of a soil. Moreover, in the Whian Whian profile, loss of aluminium by downward leaching is probably slight, due to rapid absorption by the roots in the duff layer. Sampling on a statistical basis would be necessary to decide whether, under certain circumstances (cf. Polynov 1948), vegetation may retard podsolization and loss of iron and aluminium sesquioxides. The Whian Whian profile does, however, suggest that re-deposition in litter, and re-absorption by tree roots, might account for anomalous aluminium gradients in the upper horizons of soils, provided that accumulating species have been dominant for an adequate time. Aluminium accumulators are striking examples of what Crocker (1952) calls pedogenetically effective biotypes. Retention of aluminium, partly as free alumina, is associated with the "laterization" characteristic of red basaltic soils with adequate moisture. Accumulation of suitable organic matter directly increases laterization and lowers the silica/alumina ratio. A tendency to "de-laterization" is conceivable when dominant Al accumulators are replaced by non-accumulators. There is an inverse relation between annual rainfall and silica/alumina ratio (Prescott and

Pendleton 1952). Al accumulators do not grow in rain-forests under low rainfall, e.g. on basaltic red soils at Yarraman, southern Queensland (average annual rainfall 30 in.).

A few of the accumulating trees of Australian rain-forests (e.g. *Cardwellia sublimis* F. Muell., *Ceratopetalum apetalum* D. Don., *Schizomeria ovata* D. Don.) may be considered dominant in the ecological sense. *Cardwellia* is found on red soils from granite and basalt in tropical north Queensland. Both *Ceratopetalum* and *Schizomeria* may be found in northern New South Wales on podsolics in transitional communities (with *Tristania conferta* R. Br. etc.) where *Schizomeria* appears to exercise a "constructive" function earlier in succession than *Ceratopetalum*.

Other accumulating trees of Australian rain-forests such as *Orites excelsa* R. Br. and *Helicia glabriflora* F. Muell. are much less common in communities on red soils in northern New South Wales, although their constancy is high.

Studies of the autecology of accumulators such as *Ceratopetalum apetalum*, which is an important timber tree, and of associated soil changes (movement of sesquioxides, Ca, etc.) would give an experimental value to the magnitude of "the independent plant factor" in the ecosystem considered. Present understanding of the plant factor is largely philosophical (Crocker 1952).

Known accumulating species, with few exceptions, inhabit the tropical or subtropical regions of the world, and belong to groups which, according to Bews (1927) are classed as "relatively primitive, hygrophilous or mesophytic". It is remarkable that the only monocotyledonous family (Rapataceae) in which accumulation is well developed, occupies a strictly mesic and limited tropical habitat. Other evidence to be given in the following section (e.g. Filicales, Lycopodiaceae) suggests that accumulation is often a concomitant of specialization and narrow physiological tolerances. On the other hand, accumulation is not apparently found in versatile species with relatively wide physiological tolerances.

There are several examples of positive widespread tropical species which accumulate aluminium, whereas endemic and possibly derivative species do not.

Thus *Hedyotis auricularia* L. (Rubiaceae) is widely distributed throughout the tropics, and was positive for six localities tested. Specimens of endemic *H. mitrasacmoides* F. Muell. and *H. trachymenoides* F. Muell. from numerous localities in the drier regions of Queensland were negative. Specimens from Queensland of *H. galioides* F. Muell., a rather more mesic species, were also negative. *H. auricularia* is the only species of these to contain alkaloids.

Lasianthus strigosus Wight (Rubiaceae) has a wide tropical distribution and accumulates aluminium, whereas *L. graciliflorus* Bail., endemic to Australia, does not.

Coelospermum reticulatum Benth. (Rubiaceae) is a shrub or small tree which grows in dry *Eucalyptus* woodland and in soils which are probably acid. It is positive. *C. paniculatum* F. Muell. is a vine of more restricted distribution in "xerophytic rain forests" on acid soils. It is negative. Both of these species are endemic, but the genus is well developed in the tropics to the north. If the vine habit is presumed derivative, loss of accumulation has occurred in *C. paniculatum* without obvious edaphic control.

Further, *Quintinia* (Escalloniaceae) and *Tetrasynandra* (Monimiaceae) both contain closely related species which differ markedly in aluminium content. *Quintinia verdonii* F. Muell. is constantly positive, and is found from Manning River in New South Wales to southern Queensland. The closely allied *Q. sieberi* A. DC., with two exceptions, is negative, and found from the Victorian border of New South Wales to southern Queensland, but not extending so far north as *Q. verdonii.* Two other species, *Q. fawkneri* F. Muell. and *Q. quatrefagesii* F. Muell. are confined to mountain tops in north Queensland, and are negative.

Tetrasynandra laxiflora (Benth.) Perk. and *T. pubescens* (Benth.) Perk. are closely related. The former is negative, as is *T. longipes* (Benth.) Perk. The positive *T. pubescens* is mainly distinguished by its toothed leaves from *T. laxiflora,* which has entire or subentire leaves. Toothed leaves are common in the family, and seedlings and coppice shoots of entire-leaved species bear teeth. Ontogenetically, then, accumulation in *T. pubescens* is linked with a primitive character in the group. *T. laxiflora* is found from central to north Queensland, whereas the other two species are confined to north Queensland (*T. longipes* to the lowlands).

To summarize, both *Q. verdonii* and *T. pubescens* are comparable in that they are accumulators, and the closely related species in their respective genera have wider distributions. Less closely related species have small distributions. In these cases, following the general thesis that accumulation is associated with primitive characters and is a physiological relic, both *Q. verdonii* and *T. pubescens* would be considered old, and not modern relics.

Although complete ecological observations of accumulators have not been made, it seems that, among rain-forest species in Queensland, accumulators occur in "climax" communities and late in succession. This indicates that their physiological tolerances are narrow compared with pioneer species, and with species of the "dry rain-forests", which do not accumulate.

(*c*) *Taxonomic*

The following orders and families are known to contain species which accumulate aluminium (Hutchinson 1943; Chenery 1948*a*, 1948*b*, 1949, 1951). The dicotyledons are arranged according to Hutchinson (1926).

SPERMATOPHYTA—Dicotyledons

Order Magnoliales	Family Winteraceae
Laurales	Monimiaceae
	Lauraceae
Violales	Violaceae
Polygalales	Polygalaceae
	Vochysiaceae
Lythrales	Crypteroniaceae
Thymelaeales	Geissolomataceae
Proteales	Proteaceae
Theales	Theaceae
Myrtales	Myrtaceae
	Melastomaceae
	Rhizophoraceae
Tiliales	Scytopetalaceae
Euphorbiales	Euphorbiaceae
Cunoniales	Cunoniaceae
	Escalloniaceae
	Hydrangeaceae
Celastrales	Celastraceae
	Icacinaceae
Santalales	Octoknemataceae
Juglandales	Juglandaceae
Ericales	Diapensiaceae
Styracales	Symplocaceae
	Diclidantheraceae
Loganiales	Loganiaceae
Apocynales	Apocynaceae
Rubiales	Rubiaceae
Gentianales	Gentianaceae
Personales	Lentibulariaceae

The coverage of testing by Chenery and in the present paper is not sufficiently comprehensive to regard the above list as complete, nor is the differentiation between obligate and facultative accumulators established in some instances.

A striking point about the list is the comparatively large number of small specialized tropical families which occur in widespread, otherwise negative orders, e.g. Vochysiaceae, Crypteroniaceae, Geissolomataceae, Scytopetalaceae, Octoknemataceae, Symplocaceae, and Diclidantheraceae. Further, in some families, e.g. Proteaceae, there is a striking number of monotypic isolated genera which are positive, e.g. *Austromuellera, Cardwellia, Hicksbeachia, Kermadecia,* and *Placospermum.* These small families and genera are often endemic, generally in tropical habitats. This evidence would support the view that accumulation is a physiological relic in these groups.

All the accumulating orders are listed in Figure 1, showing the probable course of evolution of the dicotyledons, suggested by Hutchinson (1926).

With the exception of Rubiales, all the well-developed accumulating orders are confined to the Archichlamydeae, or the primitive sections of Metachlamydeae (Ericales, Styracales). Accumulation is erratically developed in Rubiales, and only slightly in other Metachlamydeae (Loganiales, Personales, and Gentianales).

A notable feature of the diagram is that accumulators are absent from Hutchinson's most primitive orders, particularly the section where herbaceous habit is predominant. Thus Ranales, Berberidales, and Rhoeadales are negative, yet from them stem the positive Polygalales and Violales. Nevertheless, this apparent anomaly may be explained. The three early orders are characteristically temperate and herbaceous. Where a tropical family does occur in them (Menispermaceae in Berberidales) it is composed of vines, which are considered a derivative growth form. The positive members of Violales and Polygalales are tropical, and in the latter are arborescent, in contrast to the negative herbaceous members of temperate regions. Both orders are regarded by Hutchinson (1926) as isolated, fixed types. The above reasoning suggests that the herbaceous orders placed early in Hutchinson's diagram are not actually primitive. Indeed, it may be inferred that their primitive archetypes no longer exist.

The poor development of accumulators among early orders with arborescent habit predominant is similarly explicable. The only positive member of Magnoliales is tropical, whereas the order is generally temperate in its modern extension. Dilleniales, while a tropical or subtropical group, is rarely arborescent, and contains numerous species which are lianes, i.e. derivative forms. On the evidence of aluminium accumulation, Dilleniales would be considered comparatively advanced by reduction.

Bixales is negative, and, with the negative Dilleniales, links the feebly positive Magnoliales with the strongly positive Theales. Yet Bixales is a tropical, often arborescent order. Absence of accumulation suggests that Bixales is not well placed here, and is scarcely to be regarded as primitive.

Theales contains the positive tropical family Theaceae. Other families in the order are negative, and are also tropical, but are not generally arborescent. Dipterocarpaceae is an exception. This negative family of trees is mainly distributed over the Indo-Malayan region, but is also found in tropical Africa. Absence of accumulation suggests that Dipterocarpaceae is not one of the ancient tropical families of which Africa has so often been the centrum. Borneo, or an adjacent land now submerged, has in fact been regarded as the original home of the family (Symington 1941).

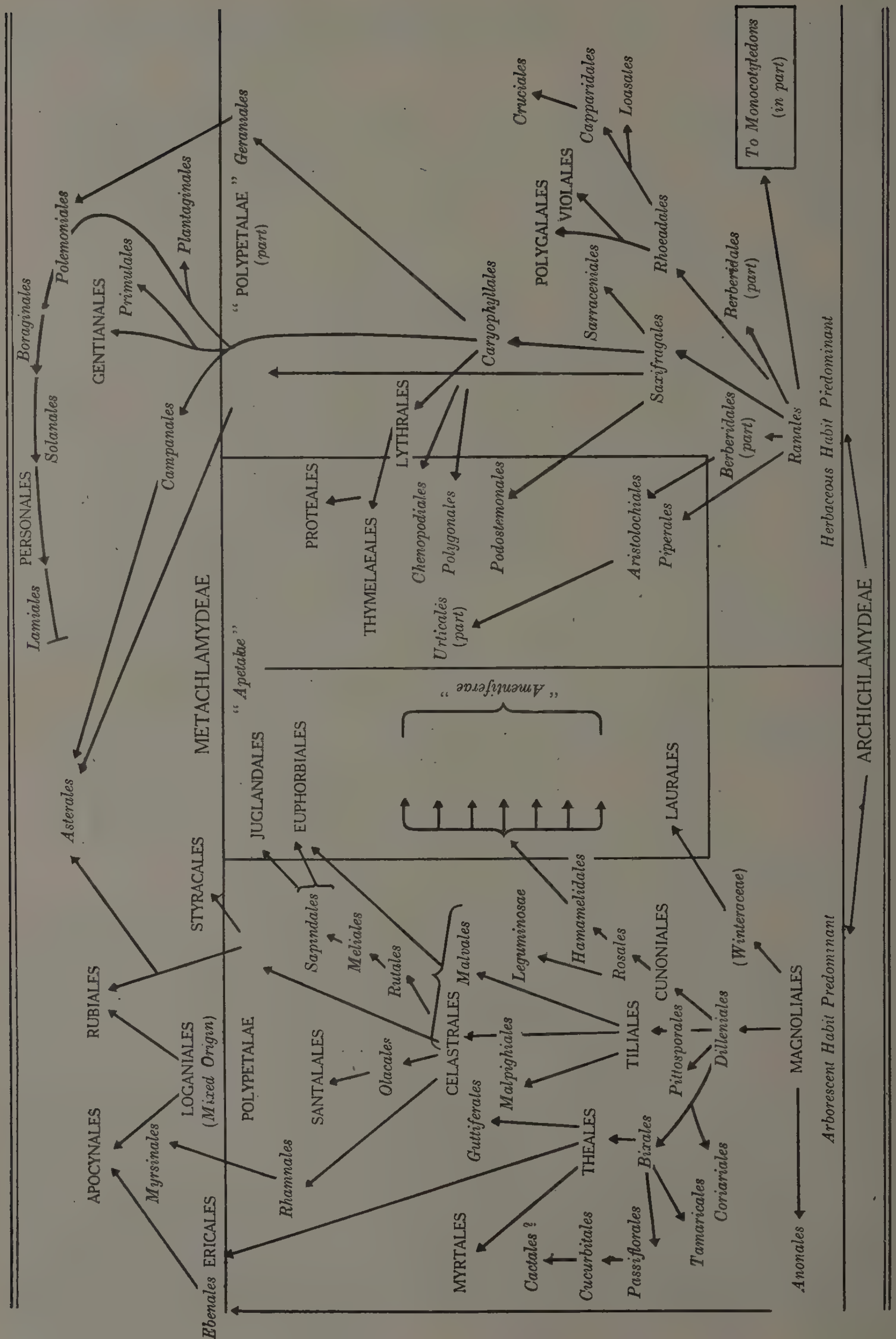

Ebenales
ERICALES
APOCYNALES
Myrsinales
LOGANIALES
(Mixed Origin)
RUBIALES
Asterales
STYRACALES
Rhamnales
POLYPETALAE
SANTALALES
Olacales
CELASTRALES
Rutales
Meliales
Sapindales
JUGLANDALES
EUPHORBIALES
Malvales
MYRTALES
Cactales ?
Cucurbitales
Passiflorales
Guttiferales
Malpighiales
THEALES
Bixales
Tamaricales
Coriariales
TILIALES
Leguminosae
Hamamelidales
Rosales
CUNONIALES
Pittosporales
Dilleniales
(Winteraceae)
MAGNOLIALES
Anonales
Arborescent Habit Predominant
ARCHICHLAMYDEAE
LAURALES
"Amentiferae"
METACHLAMYDEAE
"Apetalae"
Lamiales
PERSONALES
Solanales
Boraginales
Polemoniales
GENTIANALES
Primulales
Plantaginales
Campanales
" POLYPETALAE " (part)
Geraniales
PROTEALES
THYMELAEALES
LYTHRALES
Chenopodiales
Polygonales
Podostemonales
Urticales (part)
Aristolochiales
Piperales
Caryophyllales
Saxifragales
Sarraceniales
POLYGALALES
VIOLALES
Rhoeadales
Cruciales
Capparidales
Loasales
Berberidales (part)
Berberidales (part)
Ranales
Herbaceous Habit Predominant
To Monocotyledons (in part)

Fig. 1.—Diagram showing the probable course of evolution of the dicotyledons, after Hutchinson (1926). Aluminium-accumulating orders are shown in capitals.

Olacales, which is negative, and links the positive Celastrales and Santalales, is considered more advanced on the evidence of accumulation and by Hutchinson (1926).

Among more advanced orders in the predominantly herbaceous section of Figure 1, it is evident that a negative series of orders runs from Ranales through Saxifragales and Caryophyllales ultimately to Personales, Gentianales, or Proteales, which are positive. Both Saxifragales and Caryophyllales would not be expected to accumulate, since they are extra-tropical and typically herbaceous. Primulales and Plantaginales are also herbaceous and temperate or widely dispersed. The positive member of Gentianales is, however, of tropical distribution in a characteristically temperate herbaceous family. Polemoniales, Boraginales, and Solanales are generally herbaceous and extra-tropical. The positive *Utricularia* in Personales is a tropical and subtropical plant of aberrant habit in an otherwise widely distributed herbaceous order.

The above examples of discontinuous accumulation in Hutchinson's scheme, and the notable development of accumulation in tropical trees of ancient groups, suggest that many intermediate orders are now extinct. Thus the archetypes of tropical positive Winteraceae would be considered missing from modern floras.

Diapensiaceae provided the only example of a positive family of shrubs found in extra-tropical regions. In fact, this family is remarkable in being chiefly arctic-alpine. It has been placed, apparently with some doubt, in Ericales.

The development of accumulation among angiosperms is otherwise characteristic of tropical, more primitive groups. Lower plants, such as ferns, which accumulate, are universally distributed.

Accumulation in Thymelaeales and Proteales supports the suggestion of their close affinity, similarly for Crypteroniaceae and Escalloniaceae. The affinities on botanical grounds of Rubiaceae, Loganiaceae, and Melastomaceae are also supported by their common accumulation.

The relationship of accumulation, as a special character, will be considered in the detailed classification of several positive families which occur in Australia.

Proteaceae is divided into two subfamilies:

(i) Grevillioideae has three tribes, all containing accumulators, and tribe Grevilleae conspicuously so.

(ii) Persoonioideae has four tribes, and with the exception of Chenery's (1948*a*) single record of *Brabejum* in Persoonieae, none of the tribes is positive.

If reduction in number of seeds and ovules is considered an advance, then the positive Grevillioideae is more primitive.

Monimiaceae has six tribes which may be arranged under two subfamilies (Perkins and Gilg 1901).

(i) Monimioideae contains four tribes, each of which has accumulating species. This is treated as the more primitive group.

(ii) Atherospermoideae has two tribes, but only Siparuneae is positive. It is notable that, among Australian Monimiaceae at least, alkaloids occur only in the other tribe, Laurelieae.

Money, Bailey, and Swamy (1950) have arranged the family into four subfamilies—Hortonioideae, Atherospermoideae, Monimoideae, and Siparunoideae. Of these, only Atherospermoideae is negative. Hortonioideae has retained a relatively primitive combination of floral and vegetative characters. It would appear that Monimoideae and Siparunoideae have had an independent and partly parallel evolution from common accumulating ancestors of a *Hortonia*-like type.

In Euphorbiaceae, except for one positive species recorded in the genus *Uapaca,* all the accumulators occur in the subtribe Antidesminae of the subfamily Phyllanthoideae. *Uapaca* is the only genus in Uapacinae of this subfamily. Uapacinae is close botanically to Antidesminae, but is separated by its inflorescences bearing involucres. In Antidesminae, only one genus is negative (*Cometia*). Although the other sections of the family were fairly widely sampled, no accumulators were recorded, so that accumulation is remarkably restricted within the family Euphorbiaceae. The positive Phyllanthoideae are more primitive botanically than the subfamily Crotonoideae.

Finally, with regard to Bentham and Hooker's Saxifragaceae, this has been separated by Hutchinson (1926) into four families—Saxifragaceae, Hydrangeaceae, Escalloniaceae, and Cunoniaceae. Saxifragaceae *sensu stricto* is the only family to lack accumulation, and is predominantly herbaceous. The other three positive families are predominantly woody. This is another example supporting the thesis that accumulation is generally confined to woody types.

SPERMATOPHYTA—Monocotyledons

Tests by Chenery (1949) and present results indicate that accumulation is comparatively rare in monocotyledons. The small specialized family Rapateaceae contains numerous positive genera. *Aletris,* formerly placed in Haemodoraceae, but now in Liliaceae, also has several positive species. Chenery (1949) has an ecological explanation for the relatively low accumulation in *Aletris bracteata* Northrop. This plant is exceptional in growing on calcareous soils; the other species grow on "acid pine barren soils in which aluminium is readily available".

The monocotyledons are regarded as more advanced, generally herbaceous derivatives of dicotyledonous stocks, and are often ubiquitously distributed. It may be assumed that this history has not favoured the development or retention of accumulation.

SPERMATOPHYTA—Gymnosperms

Both the present and Chenery's (1949) results show that accumulators do not occur. Yet most of the Coniferae have cell sap acidities within the aluminium plant range (Roberts and Doyle 1938), and many grow on acid soils.

PTERIDOPHYTA

The following positive families are recorded (Chenery 1949, and present paper):

Angiopteridaceae
Cyatheaceae
Dicksoniaceae
Gleicheniaceae
Hymenophyllaceae
Isoetaceae
Loxsomaceae
Lycopodiaceae
Marattiaceae
Matoniaceae
Ophioglossaceae
Plagiogyriaceae
Polypodiaceae

Several classifications have lately been proposed for Filicales (Christensen 1938; Copeland 1947; Holttum 1949), and the most recent of these is illustrated in Figure 2.

It will be observed that accumulating families are generally primitive. Chenery (1949) has already commented upon the "fact that aluminium-accumulators are almost entirely confined to ancient families and genera" of Pteridophyta.

Four minor accumulating groups occur in the large advanced Dennstaedtiaceae. In Blechnoideae, the three accumulating species of *Blechnum* are considered anomalous because of their bipinnate fronds, a primitive character in the group. Moderate accumulation has been demontrated for only one species of *Asplenium* (Chenery 1949). Both *Athyrium* and *Asplenium* have been suggested (Holttum 1949) as likely origins for the blechnoid ferns, a suggestion supported by common accumulation. Superficially, *Blechnum* is much like *Plagiogyria,* also an accumulator. Only two species of Dryopteridoideae are recorded as moderate accumulators. Holttum prefers to associate the primitive members of this subfamily, not with Cyatheaceae as proposed by most authors, but with a dennstaedtoid source. The occurrence of aluminium accumulation would favour *Cyathea* as a prototype. Lastly, among the positive Dennstaedtiaceae, is the subfamily Lindsayoideae, which probably represents an independent development, parallel to the Dennstaedtioideae, from the same stock (Holttum 1949). The affinity of *Tapeinidium* to *Lindsaya* is close within the subfamily, with the former probably derivative. Although *Lindsaya* had not previously been found to accumulate aluminium, its affinity to the well-developed accumulator *Tapeinidium* prompted the testing of numerous specimens of various *Lindsaya* spp. In this way, two out of nine species were revealed as capable of accumulation. These were *L. decomposita* Willd. and *L. orbiculata* (Lam.) Mett. Samples of the former from 12 different localities gave tests ranging from

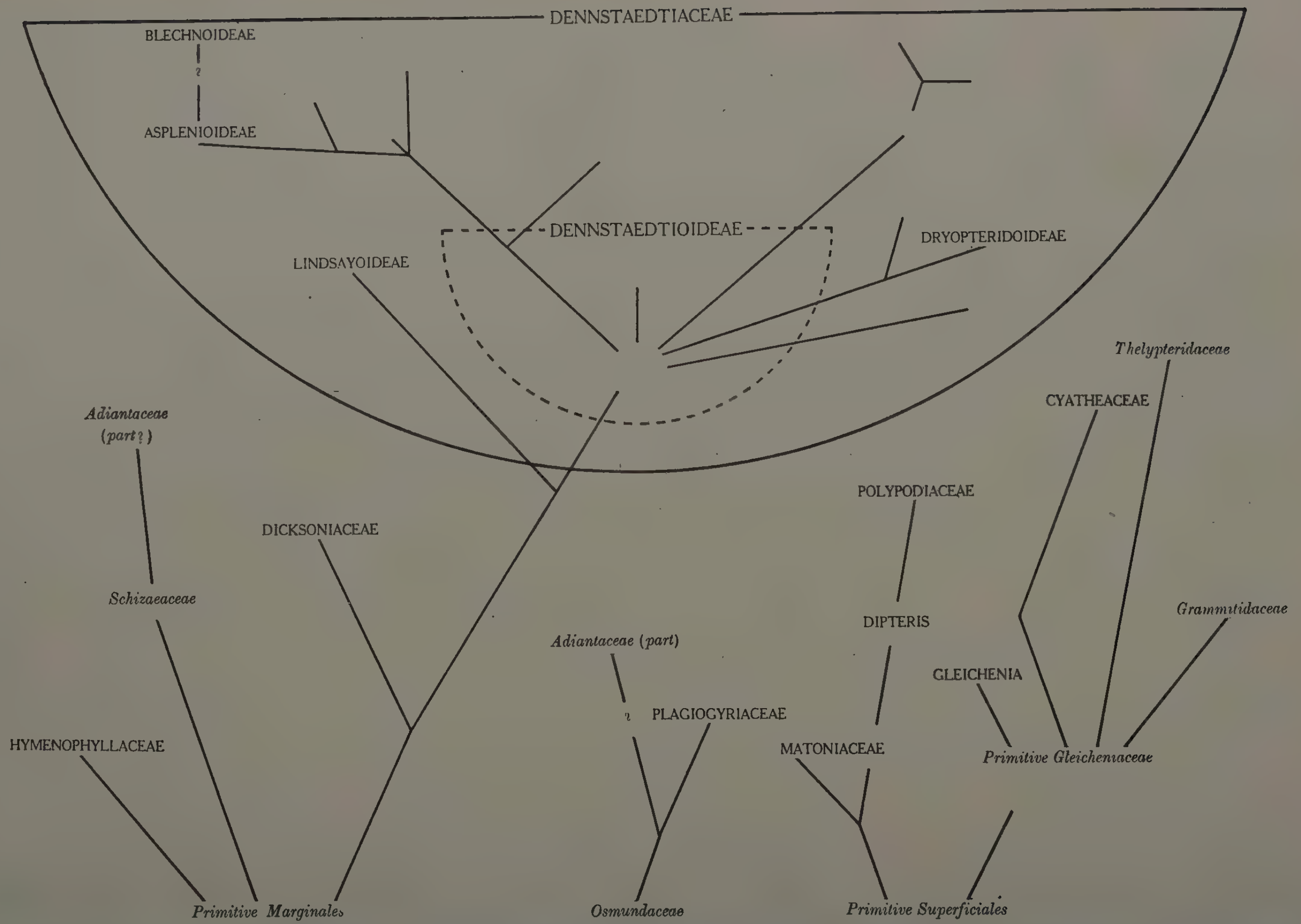

DENNSTAEDTIACEAE
BLECHNOIDEAE
?
ASPLENIOIDEAE
DENNSTAEDTIOIDEAE
DRYOPTERIDOIDEAE
LINDSAYOIDEAE
Thelypteridaceae
CYATHEACEAE
Adiantaceae
(part ?)
DICKSONIACEAE
POLYPODIACEAE
Schizaeaceae
DIPTERIS
Grammitidaceae
Adiantaceae (part)
GLEICHENIA
?
PLAGIOGYRIACEAE
HYMENOPHYLLACEAE
MATONIACEAE
Primitive Gleicheniaceae
Primitive Marginales
Osmundaceae
Primitive Superficiales

Fig. 2.—Holttum's (1949) diagram of interrelations of various fern groups (Filicales). Accumulators are in capital letters and non-accumulators omitted in Dennstaedtiaceae.

negative to > 3000 p.p.m. Al (qualitative). Similarly, several samples of *L. orbiculata* gave negative or positive results. This variation in results for certain plants has already been mentioned, and suggests that caution must be used in concluding, on the basis of limited spot-testing, that a species is an obligate accumulator, or even that accumulation does not occur under suitable conditions.

The more primitive groups of Filicales, with few exceptions, accumulate aluminium. Accumulators are not recorded in Osmundaceae, but similar cases of the apparent origination of positive from negative stocks (in linear diagrams) have already been noted for dicotyledons.

TABLE 1

Al CONTENT AND ALKALOIDS OF SELECTED LYCOPODIUM SPP.

Species	% Al in Si-free Ash	Average Mol. Wt. of Alkaloids
Group Eulycopodium		
Subgroup Clavatostachys		
Section Annotina		
L. annotinum L.	0.99-4.17	277
L. annotinum L. var. *acrifolium* Fernald	2.13-4.11	276
Section Clavata		
L. clavatum L. Europe	8.63-16.05	262
America	3.63-13.40	209
Section Obscura		
L. obscurum L. var. *dendroideum* Michx.	12.95-17.88	267
Subgroup Complanatostachys		
Section Complanata		
L. sabinaefolium Willd.	15.17-23.22	223
L. complanatum L.	20.2, 23.2	247
L. flabelliforme (Fernald) Blanchard	16.87-23.59	259
L. tristachyum Pursh.	22.22-31.36	276
Group Cernuostachys		
Section Cernua		
L. cernuum L.	17.32	212

These cases prevent the conclusion that accumulation is simply a primitive phenomenon which has become attenuated and finally lost by "reduction". On the contrary, there is some evidence to be discussed below (*Lycopodium*) which suggests the development of accumulation, as a special character, more than once in evolution.

All the genera of Marattiales are positive, supporting the acceptance by Copeland (1947) of a single family within the order.

In Lycopodiaceae, Chenery (1949) has confirmed earlier findings that the subgenus *Urostachys* contains comparatively fewer accumulators than the rest of *Lycopodium*. Data are available for the percentage of aluminium in Si-free ash (Hutchinson 1943), and formulae of alkaloids of various *Lycopodium* spp. (Henry 1949), and are shown in Table 1.

The sections are arranged in order of increasing morphological complexity (Hutchinson 1949).

It is dangerous to attempt to indicate which alkaloids are more "advanced", since chemical complexity is not necessarily synonymous with biogenetic complexity. The comparison of average molecular weights of alkaloids of each species may have some value, but its use by McNair (1934, 1935) has been justly criticized by Weevers (1943). In the present case, the alkaloids may represent a mixture of derivatives from several "ubiquitous metabolites" of varying molecular weights, and which include nicotine. With this reservation, and since biogenetic details of the alkaloids are not available, McNair's method has been used in Table 1. There is an irregular increase in aluminium content throughout the sections, with a climax at the end of Section Complanata. There is no general trend in average molecular weights of alkaloids, except for the Section Complanata, where *L. tristachyum* would be regarded as the most highly advanced species. This agrees with botanical opinion that this species is the most complex morphologically of the Section.

Analyses quoted by Hutchinson (1943) indicate that European specimens of *L. clavatum* tend to contain more aluminium than American specimens. European and American samples have also yielded different alkaloids, and have even prompted the suggestion that they may be different varieties or species (Henry 1949). A similar suggestion was made with regard to *L. annotinum* var. *acrifolium*, which yields alkaloids different from those of *L. annotinum* (Henry 1949), but the aluminium analyses scarcely support the suggestion.

Hutchinson (1943) considered that the evidence compiled for *Lycopodium* suggests "that the capacity to accumulate the element has been developed more than once in the genus".

Australian representatives from the lower cryptogams were not tested, but Chenery (1949) found that accumulation is feebly developed.

The aluminon test may also be useful in the identification, on a generic and sometimes specific level, of wood samples where other information is inadequate. The specificity of the aluminium test was illustrated in Queensland species of *Helicia*. All the species gave positive tests except *H. cribbiana* F. M. Bail., and this tree is now regarded as wrongly placed in the genus. It is interesting to note that *Finschia,* with the floral characters of *Grevillea* (negative) and fruit of *Helicia* (positive), is negative.

V. ACKNOWLEDGMENTS

The author is indebted to Dr. H. E. Dadswell, of the Division of Forest Products, C.S.I.R.O., Melbourne, for the photomicrographs, and to the Queensland Government Botanist (Mr. W. D. Francis) for permission to test herbarium specimens. Mr. L. S. Smith, Botanist of the

Queensland Herbarium, Brisbane, gave valuable advice concerning the critical systematics of several of the groups. Miss P. Macarthur and Mr. J. G. Tracey are thanked for their assistance in the routine tests. The helpful criticism of those who read the typescript is gratefully acknowledged.

VI. References

Amos, G. L., and Dadswell, H. E. (1948).—Siliceous inclusions in wood in relation to marine borer resistance. *J. Coun. Sci. Industr. Res. Aust.* **21**: 190-6.

Amos, G. L. (1952).—Silica in timbers. C.S.I.R.O. Aust. Bull. No. 267.

Bews, J. W. (1927).—"Studies in the Ecological Evolution of the Angiosperms." 134 pp. (Wheldon & Wesley Ltd.: London.)

Campbell, W. G., Packman, D. F., and Rolfe, D. M. (1945).—The composition and origin of a white deposit found in galleries of a wood-boring insect in two samples of the wood of *Qualia* sp. *Emp. For. J.* 24 (2): 232-3.

Chenery, E. M. (1946).—Aluminium in trees. *Emp. For. J.* 25 (2): 255-6.

Chenery, E. M. (1948*a*).—Aluminium in the plant world. I. *Kew Bull.* **2**: 173-83.

Chenery, E. M. (1948*b*).—Aluminium in plants and its relation to plant pigments. *Ann. Bot.* **12**: 121-36.

Chenery, E. M. (1949).—Aluminium in the plant world. II, III. *Kew Bull.* **4**: 463-73.

Chenery, E. M. (1951).—Some aspects of the aluminium cycle. *J. Soil. Sci.* 2 (1): 97-109.

Christensen, C. (1938).—'Filicinae', Chap. xx in Verdoorn, "Manual of Pteridology." (M. Nijhof: The Hague.)

Copeland, E. B. (1947).—"Genera Filicum." 247 pp. + pls. (Chronica Botanica: Waltham, Mass.)

Crocker, R. L. (1952).—Soil genesis and pedogenic factors. *Quart. Rev. Biol.* 27 (2): 139-68.

Gilbert, B. E., and Pember, F. R. (1935).—Tolerance of certain weeds and grasses to toxic aluminium. *Soil Sci.* **39**: 425-9.

Henry, T. A. (1949).—"The Plant Alkaloids". 804 pp. (J. & A. Churchill: London.)

Holttum, R. E. (1949).—The classification of ferns. *Biol. Rev.* **24**: 267-96.

Hutchinson, G. E. (1943).—The biogeochemistry of aluminium and of certain related elements. *Quart. Rev. Biol.* **18**: 1-29, 128-53, 242-62, 331-63.

Hutchinson, G. E. (1945).—Aluminium in soils, plants and animals. *Soil Sci.* **60**: 29-40.

Hutchinson, J. (1926).—"The Families of Flowering Plants." I. Dicotyledons. 328 pp. (Macmillan: London.)

Keller, W. D. (1949).—*Econ. Geol.* **44**: 451-4. (*Chem. Abstr.* **45**: 3911^i (1951).)

Leeper, G. W. (1952).—"Introduction to Soil Science." 222 pp. (University Press: Melbourne.)

McNair, J. B. (1934).—The evolutionary status of plant families in relation to some chemical properties. *Amer. J. Bot.* **21**: 427-52.

McNair, J. B. (1935).—Angiosperm phylogeny on a chemical basis. *Bull. Torrey Bot. Cl.* **62**: 515-32.

Maiden, J. H., and Smith, H. G. (1895).—On a natural deposit of aluminium succinate in the timber of *Grevillea robusta* R. Br. *Proc. Roy. Soc. N.S.W.* **29**: 325-35.

Metcalfe, C. R., and Chalk, L. (1950).—"Anatomy of the Dicotyledons." Vols. I and II. 1500 pp. (Clarendon Press: Oxford.)

Money, L. L., Bailey, I. W., and Swamy, B. G. C. (1950).—The morphology and relationships of the Monimiaceae. *J. Arnold Arbor.* 31 (4): 372-404.

Muir, A. (1950).—Biogeochemistry of aluminium. Rothamst. Exp. Sta., Lawes Agric. Trust, Rep. 1949, p. 40.

PERKINS, J., and GILG, E. (1901).—"Das Pflanzenreich". (Engelmann: Leipzig.)

POLYNOV, B. (1948).—*Pedology* 3, abstr. 1948. *Soils & Fert.* No. 1491. (Cited by Chenery 1951.)

PRESCOTT, J. A., and PENDLETON, R. L. (1952).—Laterite and lateritic soils. Bur. Soil Sci., Harpenden, Tech. Commun. No. 47.

ROBERTS, O., and DOYLE, J. (1938).—The pH of conifer leaves in relation to systematy. *Sci. Proc. R. Dublin Soc.* 21: 655. (Cited by Chenery 1949.)

ROBINSON, W. O., and EDGINTON, G. (1945).—Minor elements in plants, and some accumulator plants. *Soil Sci.* **60**: 15-28.

SMITH, H. G. (1903).—Aluminium, the chief inorganic element in a proteaceous tree, and the occurrence of aluminium succinate in trees of this species. *Proc. Roy. Soc. N.S.W.* 37: 107-20.

SYMINGTON, C. F. (1941).—"Foresters' Manual of Dipterocarps." Malayan For. Rec. No. 16. 244 pp. (Caxton Press Ltd.: Kuala Lumpur.)

WEBB, L. J. (1952).—Occurrence of aluminium succinate in *Cardwellia sublimis* F. Muell. *Nature* 171: 656.

WEEVERS, T. L. (1943).—The relation between taxonomy and chemistry of plants. *Blumea*: 412-22.

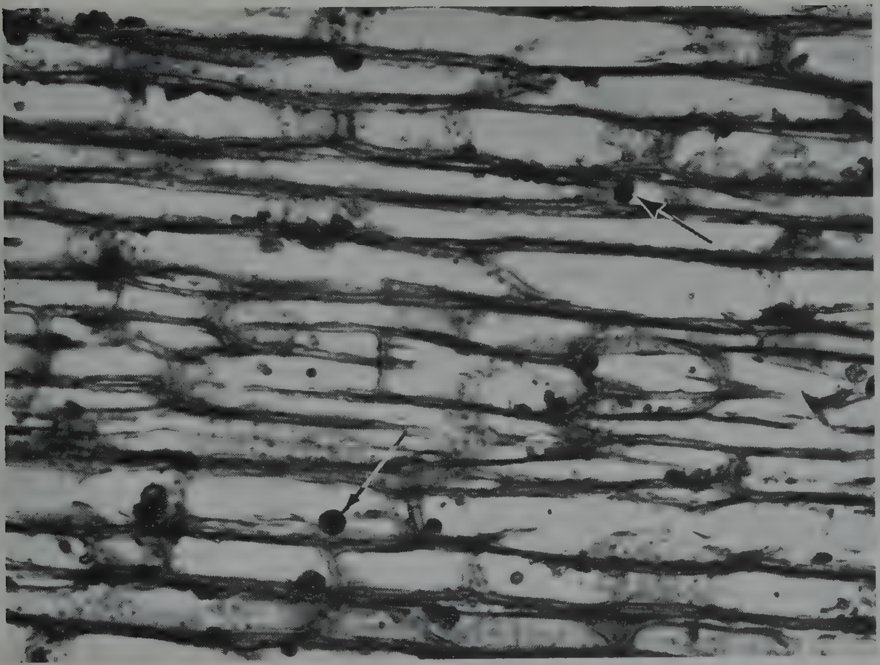


Fig. 1.—Characteristic aluminous deposits in ray cells of *Cardwellia sublimis* F. Muell. × 225.

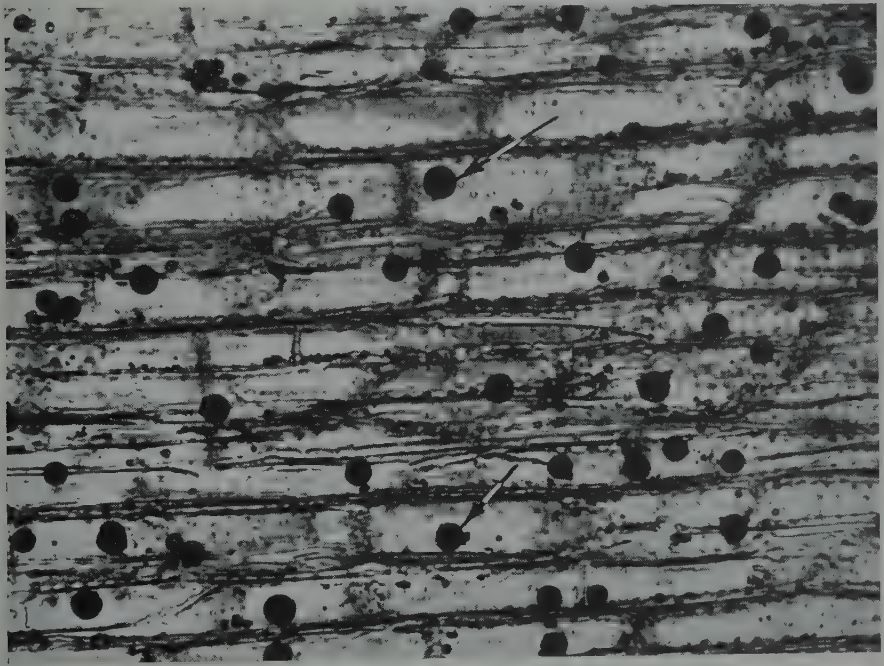


Fig. 2.—Characteristic aluminous deposits in ray cells of *Orites excelsa* R. Br. × 225.

SOME DICOTYLEDONOUS POLLEN TYPES FROM CAINOZOIC DEPOSITS IN THE AUSTRALIAN REGION

By Isabel C. Cookson* and Kathleen M. Pike*

(*Manuscript received January 7, 1954*)

Summary

Pollen types referable to the families Casuarinaceae, Haloragaceae, Myrtaceae, Olacaceae, ?Proteaceae, Santalaceae, and Sapindaceae have been described from Cainozoic deposits in the Australian region; their relationship to living species has been discussed wherever possible.

The characters and distribution of three sporomorphs of uncertain affinity have been considered.

Details concerning the pollen grains of some of the living species of *Anacolosa*, *Cathedra*, *Casuarina*, the tribe Cupanieae (Sapindaceae), *Haloragis*, *Myriophyllum*, and *Santalum* have been recorded.

I. Introduction

The present paper is concerned with the identification and diagnosis of some of the many undescribed pollen types that are preserved in Australian Cainozoic deposits. Some of these can be related to families and genera still living in the Australian region or Pacific islands; others apparently represent plants now extinct.

The nomenclature adopted is the same as that used in earlier publications (Cookson 1953). Most of the pollen residues have been obtained by the chlorination-acetolysis method with a pre-treatment with hydrofluoric acid when necessary. Acetolysed pollen grains of living types have been used for comparison with the fossil forms.

II. Location and Age of Sediments

The sediments in which the fossil pollen grains have occurred are of diverse type, age, and situation in Australia, Tasmania, and southern New Guinea. The locations of the more important deposits are listed below and shown in Figure 1.

WESTERN AUSTRALIA: Brookes Inlet. Earthy lignite. Age: probably Upper Tertiary. Geol. Dept. Univ. W. Aust. No. 6643.

Denmark, 8-9 miles from. Brown coal (surface material). Age: probably Upper Tertiary. Geol. Dept. Univ. W. Aust. No. 4487.

Hay-Denmark railway, deviation at 354 miles. Carbonaceous sandy deposits from bores. Geol. Dept. Univ. W. Aust. No. 8662. Age: probably Lower Tertiary. Sample 8662/1, 50 ft below surface, "coffee rock". Sample 8662/9, from No. 9 bore.

Nornalup Inlet. Lignite. Age: probably Lower Tertiary. Geol. Dept. Univ. W. Aust. No. 32982.

---

* Botany Department, University of Melbourne.

Shannon River. Lignite. Age: probably Upper Tertiary. Geol. Dept. Univ. W. Aust. No. 40.

SOUTH AUSTRALIA: Canopus Station, near the S. Aust. and N.S.W. border, *c.* 45 miles north of the River Murray. Carbonaceous sandstone from the S.A. Dept. of Mines bore 1 at 881-910 ft. Age: Lower Tertiary.

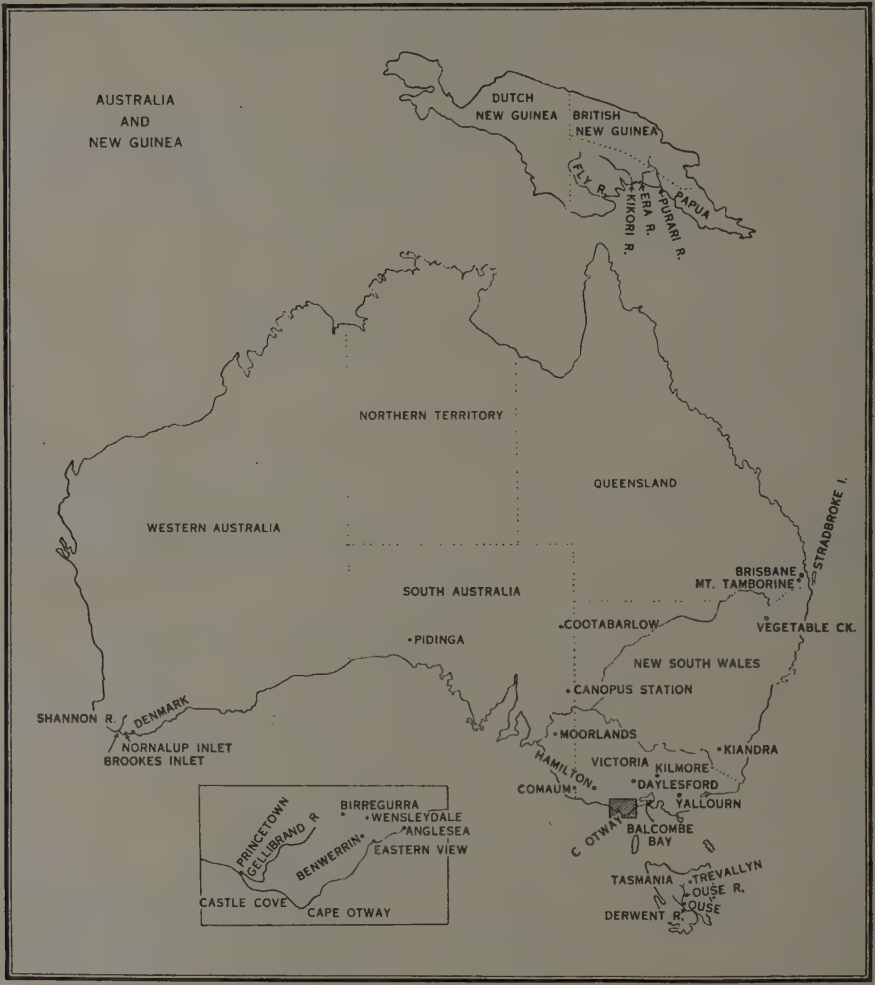

AUSTRALIA
AND
NEW GUINEA
DUTCH
NEW GUINEA
BRITISH
NEW GUINEA
FLY R.
KIKORI R.
ERA R.
PURARI R.
PAPUA
NORTHERN TERRITORY
QUEENSLAND
WESTERN AUSTRALIA
STRADBROKE I.
BRISBANE
MT. TAMBORINE
SOUTH AUSTRALIA
•COOTABARLOW
VEGETABLE CK.
•PIDINGA
NEW SOUTH WALES
•CANOPUS STATION
SHANNON R.
DENMARK
NORNALUP INLET
BROOKES INLET
•MOORLANDS
•KIANDRA
HAMILTON
VICTORIA
KILMORE
COMAUM
•DAYLESFORD
YALLOURN
C OTWAY
BALCOMBE
BAY
TASMANIA
TREVALLYN
OUSE R.
OUSE
DERWENT R.
BIRREGURRA
•WENSLEYDALE
ANGLESEA
PRINCETOWN
GELLIBRAND R
BENWERRIN
EASTERN VIEW
CASTLE COVE
CAPE OTWAY

Fig. 1.—Map showing the location of deposits in which sporomorphs have been found. (Prepared by the Geological Survey of Victoria.)

Comaum. Brown coal from S.A. Dept. of Mines bore at 619 ft 6 in. Age: Lower Tertiary (Cookson 1953).

Cootabarlow, east of Lake Frome. Carbonaceous shale from S.A. Dept. of Mines bore at 515-537 and 537-538 ft. Age: probably Lower Tertiary.

Moorlands. Brown coal. Age: ?Oligocene.

Pidinga, south of Ooldea. Lignite from S.A. Dept. of Mines bore p.15 at 11-16 ft, 31-34 ft. 6 in.; 35 ft. 6 in.-41 ft. 6 in. Age: Probably Lower Tertiary.

VICTORIA: Anglesea. Black carbonaceous sandstone from coastal cliff near mouth of Anglesea River. Age: ?Middle Eocene (Raggatt and Crespin 1952).

Bacchus Marsh. Brown coal from Lucifer Mine. Age: ?Oligocene.

Balcombe Bay. Mudstone containing leaf remains, from coastal cliff. Age: Pre-Miocene.

Bambra. Lignite from Vic. Dept. of Mines bore at 106-110 ft. Age: Lower Tertiary.

Benwerrin, south-western Victoria. Brown coal. Age: probably Lower Eocene.

Berwick. Clay underlying older volcanics at Wilson's Quarry. Age: ?Oligocene. Nat. Mus. Vic. No. P.15680.

Birregurra, south-western Victoria. Carbonaceous clay from Vic. Dept. of Mines bore 1 at 760-1020 ft. Age: Eocene (Cookson 1954*b*).

Castle Cove, Aire coast. Basal carbonaceous sandy clay, Johanna sands. Age: Upper Eocene or older (*fide* O. P. Singleton).

Coode I, near mouth of River Yarra. Carbonaceous clay. Age: pre-Pliocene.

Dilwyn Clay, Wangarrip Group, 1 mile SE. of mouth of Gellibrand River, near Princetown. Carbonaceous sandy clay. Age: Eocene (Baker 1953).

Eastern View. Lignite from Coal Mine Creek, 3½ and 5 ch upstream from Great Ocean Road. Age: Paleocene to Lower Eocene (Raggatt and Crespin 1952).

Elwood, shore-line between Marine Av. and Dickens St., St. Kilda, near Melbourne. Dark grey silty clay. Age: Quaternary.

Gellibrand River, about ¾ mile SE. of Point Ronald, near Princetown. Carbonaceous sandstone, comprising the Princetown Member. Age: Eocene (Baker 1953).

Hamilton. Carbonaceous clay from north bank of Grange Burn. Age: Upper Pliocene (Gill 1952).

Kilmore. Grey carbonaceous shale. Age: ?Upper Tertiary. Nat. Mus. Vic. No. P.15724.

Lal Lal. Carbonaceous clay from Vic. Dept. of Mines bores. Age: ?Eocene.

Maryvale, Latrobe Valley. Ligneous clay from Vic. Dept. of Mines bores. Age: Oligocene.

Moyne River, near Rosebrook Bridge, western Victoria. Clay. Age: Quaternary (Gill 1953). Nat. Mus. Vic. No. P.15586.

Nelson, Parish of Glenelg. Carbonaceous sediments from Vic. Dept. of Mines bore, SW. end of bridge over Glenelg River. Age: Lower Tertiary.

Pebble Point Formation. Basal grits, Wangarrip Group. From NW. side of Point Bell, 2¾ miles SE. of mouth of Gellibrand River, near Princetown. Age: Eocene with Paleocene affinities (Baker 1953).

Stony Creek basin, near Daylesford. Dark and light shales and clays. Age: ?Middle Pliocene (Coulson 1950).

Wensleydale. Clay parting in brown coal. Age: Lower Tertiary. Geol. Surv. Vic. No. 50083.

Yallourn. Brown coal at various horizons in the Open Cut. Age: Oligocene (Thomas and Baragwanath 1949).

Yallourn North. Brown coal (Latrobe Seam). Age: Oligocene.

TASMANIA: Edward's Farm, Mella, near Smithton. Carbonaceous sandy deposit. Coll. E.D. Gill. Age: Pleistocene.

Ouse. Lignitic seam in Ouse River about 400 yd upstream from Bridge Hotel. Age: Lower Tertiary.

Trevallyn. Pre-basaltic clay from bore 2003, investigation bore. Age: Lower Tertiary.

NEW SOUTH WALES: Kiandra, New Chum Hill. Soft ligneous shale, 135 ft below the basalt. Portion of Dr. Dulhunty's coal sample 103. Age: Lower Tertiary. Nat. Mus. Vic. No. 15710.

Vegetable Creek (Emmaville). Mudstone from Deep Leads. Age: Oligocene (Singleton 1941). Melb. Univ. Geol. Dept. No. 890.

QUEENSLAND: Mt. Tamborine. Carbonaceous clay under basalt about 300 yd below Curtis Falls, Cedar Creek. Age: Pliocene (Bryan and Jones 1946).

Stradbroke I. Black coal. Age: probably post-Miocene.

NEW GUINEA: Era River, north of delta area, between Kikori and Purari Rivers. Coal. Age: Pliocene.

Orloli Region, east of Lower Purari River. Coal. Age: Pliocene.

Shu Creek, a tributary of the Era River, south coast of Papua. Coal from a bore sunk by Australasian Petroleum Company at 525 ft. Age: Pliocene.

III. DESCRIPTIONS AND AFFINITIES OF FOSSIL POLLEN GRAINS

(*a*) *Casuarinaceae*

Plate 1, Figs. 1-6

Casuarinidites n. spt.

Grains similar to those of living species of *Casuarina,* small to medium, oblate, triangular in polar view with convex sides; angulaperturate, the pores circular, about 2 μ in diameter, usually strongly aspidate. Exine 1-2.5 μ thick, sometimes slightly thickened around the pores; sexine thicker than nexine, smooth or very finely and indistinctly patterned.

Casuarinidites cainozoicus n. spm.

Plate 1, Figs. 1-3

As for sporotype; 22-36 μ in equatorial diameter.

Known range.—Eocene to Quaternary.

WESTERN AUSTRALIA: Denmark 4487; 8662/1; 8662/9.

SOUTH AUSTRALIA: Moorlands; Pidinga 11-16 ft, 35 ft 6 in. to 41 ft 6 in.

VICTORIA: Anglesea; Bacchus Marsh; Hamilton; Kilmore; Moyne River; Stony Creek; Wensleydale; Yallourn.

TASMANIA: Ouse River.

NEW SOUTH WALES: Kiandra; Vegetable Creek.

QUEENSLAND: Stradbroke I.

Affinity.—In relating the Australian fossil pollen grains with the above characters to *Casuarina,* due consideration has been given to the existence of a closely similar type of grain in the families Betulaceae, Juglandaceae, Loganiaceae, and Myricaceae (Erdtman 1952). However, in view of the close morphological approximation of the sporomorph *Casuarinidites cainozoicus* to pollen grains of the living species of *Casuarina,* the wide distribution and large number of species of this genus in the present Australian flora, and the occurrence of well-authenticated macroscopic remains in Australian Oligocene (Pike 1952) and Pliocene (Patton 1936) deposits, there seems no reason to suspect that the pollen grains in question are those of northern types such as the Betulaceae and Juglandaceae. The family Myricaceae, on the other hand, has one representative in the southern hemisphere, namely the monotypic genus *Canacomyrica* Guill., the pollen grains of which possibly could be mistaken for those of *Casuarina*. However, examination of the grains of living species of *Casuarina* has shown that on the whole they are smaller (Appendix I) and have more strongly aspidate pores and a less strongly patterned exine than those of *Canacomyrica monticola* Guill. (27-40, av. 34 μ; Plate 2, Fig. 100).

(*b*) *Haloragaceae*

Plate 1, Figs. 7-11

Gunnerites n. spt.

Fossil pollen grains resembling those of the living species of *Gunnera;* medium-sized, spherical to subspherical, tricolpate, with bulging mesocolpia. Exine finely reticulate.

Gunnerites reticulatus Cookson, comb. nov.

Plate 1, Figs. 18, 19

Tricolpites reticulata Cookson in Brit. Aust. N.Z. Antarctic Exped. 1927-1931. Rep. A.2. (8): 134, fig. 45 (1947).

Description.—As for the sporotype; equatorial diameter 26-40 μ.

Occurrence and known range.—Kerguelen Archipelago (Lower Tertiary). New Guinea—Era River; Orloli Region; Shu Creek (Pliocene).

Comments.—As the result of a study of the pollen grains of several southern living species of *Gunnera,* it is now possible to confirm the suggestion made by Selling (1948, p. 153) that the sporomorph *Tricolpites reticulata* Cookson from Early Tertiary Kerguelen lignites is related to *Gunnera*. The pollen grains of *G. arenaria* Cheeseman, *G. cordifolia* Hook. f., *G. macrophylla* Blume, *G. monoica* Raoul, and *G. strigosa* Colenso are remarkably similar to one another in size, form, and sculpture, and in all these features are closely approached by the Kerguelen sporomorph. It is suggested therefore, that in future *Tricolpites reticulata* should be known as *Gunnerites reticulatus*. No records have been found of the occurrence of *Gunnera* in the present flora of the Kerguelen Archipelago.

A second fossil occurrence of *Gunnera* pollen has recently been discovered in Pliocene deposits of southern New Guinea. However, in view of the uniformity existing amongst the pollen grains of living species it seems preferable to associate both the New Guinea and Kerguelen examples in the sporomorph *Gunnerites reticulatus* rather than to distinguish them as separate forms on account of their widely situated locations. *Gunnera macrophylla* is the present representative of the genus in New Guinea. Fossil *Gunnera* pollen has been recorded by Auer (1933) from late Glacial deposits in Tierra del Fuego and by Selling (1947) from late Quaternary deposits in the Hawaiian Is.

Haloragacidites Couper

Pollen grains closely resembling those of Australian species of *Haloragis* and *Myriophyllum* have been seen in Tertiary residues examined during the present investigation. However, since Couper (1953) reports that an overlap in characters occurs in the pollen grains of New Zealand species of both genera, it seems advisable to refer both the Australian fossil types to the genus *Haloragacidites,* introduced by Couper (1953) for "those fossil pollen grains belonging to the family Haloragaceae that cannot be more accurately placed".

Haloragacidites haloragoides n. spm.

Plate 1, Figs. 7-9

Grains 23-40 μ in equatorial diameter, with an angular amb, pores 4-6, at the angles, projecting slightly beyond the surface of the grain. Exine 2-4 μ, considerably thicker around the pores, pattern finely granular.

Known range.—Pliocene to Quaternary.

WESTERN AUSTRALIA: Brookes Inlet; Denmark 4487; Shannon River.
VICTORIA: Elwood; Hamilton; Kilmore; Stony Creek.
QUEENSLAND: Stradbroke I.

Comments.—There appear to be no other records of fossil pollen grains identical with those of living species of *Haloragis.* Coupers' type *Haloragacidites trioratus* from New Zealand Oligocene deposits bears no resemblance to *H. haloragoides.*

The apparent absence of *H. haloragoides* from Australian Lower Tertiary deposits and its incoming in Pliocene deposits, such as those at Hamilton and Daylesford, Vic. (Cookson 1954*a*), suggest that the age of the freshwater sediments at Brookes Inlet and Shannon River, W.A., and at Stradbroke I., Queensland, is probably Pliocene or younger.

Haloragacidites haloragoides n. spm.

Plate 1, Figs. 7-9

Grains 20-34 μ in equatorial diameter; amb circular to sub-polygonal; pores 3-5, circular, 5-7 μ, aspidate, sometimes unequally spaced. Exine thin, *c.* 1-2 μ, thicker around the pores, pattern faintly verrucate.

Known range.—Pliocene.

NEW GUINEA: Orloli Region, Shu Creek.

Comments.—Only one reference to the present occurrence of *Myriophyllum* in New Guinea has been found. This is the description of *M. pygmaeum* by Mattfeld (1939). Unfortunately material of this species has been unprocurable for examination. Of the pollen grains of living Australian species available for comparison (Table 1), those of *M. verrucosum* Lindl. are the ones most closely resembling the sporomorph *Haloragacidites myriophylloides.*

Pollen grains of *Myriophyllum* are common fossils in Post-Glacial deposits in Europe (Erdtman 1943) and high frequencies of them have been reported by Auer (1933) in Post-Glacial sediments from Tierra del Fuego. Records from Tertiary deposits have been made by Wodehouse (1933) and Couper (1953).

The occurrence, in relatively large numbers, of the sporomorph *H. myriophylloides* with pollen of *Gunnera* in Pliocene beds in New Guinea recalls the similar association found by Auer in Tierra del Fuego.

TABLE 1

MORPHOLOGICAL CHARACTERS OF SOME AUSTRALIAN SPECIES OF MYRIOPHYLLUM

Species	Source of Material	Equatorial Diameter (μ)	No. of Pores	Exine Pattern
Myriophyllum elatinoides Gaud.	Jeparit, Vic., ex Herb. Melb.	23-27	3-4*-5	Very faintly and finely verrucate
M. longibracteolatum Shindl.	Bulhadelah, N.S.W., ex Melb. Univ. Herb.	29-38	3-4*-5	Coarsely verrucate
M. pedunculatum Hook.	Clarence R., N.S.W., ex Melb. Univ. Herb.	18-34	5-6	Very coarsely verrucate
M. propinquum A. Cunn.	Launceston, Tas., ex Melb. Univ. Herb.	25-31	3*-4	Finely verrucate
M. tillaeoides Diels	Ex Herb. Syd. No. 10029.	25-30	4*-5	Coarsely verrucate
M. verrucosum Lindl.	Mt. Surprise, Qld., ex Herb. Bris.	20-27	3-4*-5	Finely verrucate

* Indicates the pore number of greatest frequency.

(*c*) *Myrtaceae*

Plate 1, Figs. 21-46

The reference of fossil pollen grains either to the family Myrtaceae or to the individual genera or species comprising it is difficult and should be treated with considerable reserve for the following reasons:

(1) The small, triangular, 3-colporate pollen grains with more or less prominent arci characteristic of the Myrtaceae are paralleled closely in some genera of the Sapindaceae. When, as by analogy with the present Australian flora, endemic members of both families are likely to have been present, the difficulty in assigning fossil grains to the Myrtaceae is still further increased.

(2) The pollen grains of living myrtaceous genera cannot always be readily distinguished from one another. Thus, for example, a comparatively close similarity exists between the pollen grains of certain species of *Eucalyptus* and *Pleurocalyptus; Piliocalyx* and *Regelia; Melaleuca* and *Beaufortia; Leptospermum, Kunzea,* and *Backhousia.*

(3) Considerable variation both in size of grain and prominence of sculpture frequently occurs amongst the species of one genus, e.g. *Melaleuca ericifolia* Sm. and *M. radula* Lindl.; *Regelia inops* Schau. and *R. ciliata* Schau.

Notwithstanding such inconsistencies it is possible to recognize a few regularly occurring types with strong myrtaceous affinities in Australian Cainozoic deposits. However, in view of the above, it is proposed to refer these forms to one generalized sporotype, *Myrtaceidites*, rather than to individual genera of the family.

Myrtaceidites n. spt.

Grains small to medium, triangular to subtriangular in polar view with straight, slightly concave, or slightly convex sides; angulaperturate; tricolporate; oblate to subspheroidal; arci distinct, enclosing or not enclosing polar islands. Exine smooth, granular or finely and indistinctly patterned, never clearly reticulate.

Myrtaceidites eugeniioides n. spm.

Plate 1, Figs. 21-26

Grains small, 9-14 μ in equatorial diameter; amb with straight or slightly concave sides and truncate apices. Arci distinct, enclosing small polar islands. Exine psilate or faintly mottled.

Known range.—Eocene to Pliocene.

SOUTH AUSTRALIA: Comaum, 619 ft 6 in.; Cootabarlow, 515-537 ft; Pidinga, 11-16 ft.

VICTORIA: Anglesea; Birregurra 760 ft, 842-843 ft; Maryvale B.155, 552 ft; Yallourn North; Yallourn Fruit Zone at base of coal.

TASMANIA: Ouse River.

NEW SOUTH WALES: Vegetable Creek.

QUEENSLAND: Mt. Tamborine.

Affinity.—In its small size, truncate apices, and straight or slightly concave sides of the amb, this sporomorph agrees with pollen grains of living members of the tribe Eugeniinae. It resembles most closely pollen of *Eugenia* and *Cleistocalyx*, more particularly the small (10-15 μ) pollen grains of certain species of *Cleistocalyx* such as *C. operculatus* (Roxb.) Merr. & Perr., *C. myrtoides* (A. Gray) Merr. & Perr., and *C. seemannii* (A. Gray) Merr. & Perr.

Myrtaceidites eucalyptoides n. spm.

Plate 1, Figs. 38-46

Comments.—Since the pollen grains of living species of *Eucalyptus* cannot always be clearly distinguished from those of other genera of the Myrtaceae with straight sides, distinct arci, and equatorial diameters between 15 and 36 μ, the identification of fossil pollen grains with this genus is not altogether easy. However, some species of *Eucalyptus*

(27 out of the 75 species examined by K.M.P.) have pollen grains that are distinguishable by a decided and constant thickening of the exine around the apertures. The presence of this feature, in conjunction with other eucalyptoid characters, in some of the myrtaceous pollen grains occurring in Australian Cainozoic deposits suggests therefore that their probable affinity is with *Eucalyptus*. It is for pollen grains such as these that the generalized sporomorph *Myrtaceidites eucalyptoides* is now proposed. Two forms have been distinguished, each of which in all probability includes pollen grains of more than one species.

Myrtaceidites eucalyptoides n. spm.

Grains small to medium, 15-30 μ in equatorial diameter; amb with convex, straight, or concave sides; oblate to subspheroidal; arci prominent, enclosing or not enclosing polar islands. Exine *c.* 1 μ, thicker around the apertures; obscurely patterned, rarely psilate.

Known range.—Pliocene to Pleistocene.

Myrtaceidites eucalyptoides forma *orthus* forma nov.

Plate 1, Figs. 38-40

Grains 15-26 μ; amb with straight to slightly concave sides. Polar islands of variable size. Exine mottled.

WESTERN AUSTRALIA: Brookes Inlet; Denmark 4487.
VICTORIA: Elwood; Stony Creek.
TASMANIA: Smithton.
QUEENSLAND: Stradbroke I.

Myrtaceidites eucalyptoides forma *convexus* forma nov.

Plate 1, Figs. 41-46

Grains 17-30 μ; amb with more or less convex sides; arci distinct, enclosing or not enclosing polar islands. Exine smooth or obscurely patterned.

WESTERN AUSTRALIA: Brookes Inlet; Denmark 4487; Shannon River.
VICTORIA: Hamilton.
TASMANIA: Smithton.
QUEENSLAND: Stradbroke I.

Myrtaceidites mesonesus n. spm.

Plate 1, Figs. 32-36

Grains small, 12-23 μ in equatorial diameter; amb with straight or slightly convex sides; arci prominent, enclosing distinct polar islands. Exine *c.* 1 μ, of uniform thickness, definitely patterned but type of sculpture obscure.

Known range.—Eocene to Pliocene.

WESTERN AUSTRALIA: Hay-Denmark railway, 8662/1; Brookes Inlet; Nornalup.

SOUTH AUSTRALIA: Pidinga, 11-16 ft.

VICTORIA: Anglesea; Bacchus Marsh; Maryvale B.155, 552 ft; Yallourn, Latrobe and Yallourn Seams.

TASMANIA: Ouse River.

NEW SOUTH WALES: Kiandra; Vegetable Creek.

QUEENSLAND: Mt. Tamborine.

NEW GUINEA: Era River; Shu Creek.

Affinity.—Uncertain. Some of the larger examples (Plate 1, Fig. 36) of *M. mesonesus* are morphologically close to certain species of *Eucalyptus*, such as *E. tessellaris* F. Muell. (Plate 1, Fig. 37), in which the exine is unthickened around the apertures. However, the connection between *M. mesonesus* and *Eucalyptus* is not sufficiently clear to confirm the records by Chapman (1926) and Paterson (1935) of *Eucalyptus* leaves in Victorian Oligocene deposits.

Myrtaceidites parvus n. spm.

Grains small, 9-14 μ in equatorial diameter; amb subtriangular with convex sides; arci present which may or may not enclose polar islands. Exine psilate, indistinctly patterned or granular.

Myrtaceidites parvus forma *nesus* forma nov.

Plate 1, Figs. 29-31

Grains 10-14 μ in equatorial diameter; arci prominent, enclosing distinct polar islands; exine with granular pattern.

Known range.—Eocene to Pliocene.

SOUTH AUSTRALIA: Pidinga, 35 ft 6 in.-41 ft 6 in.

VICTORIA: Anglesea; Kilmore; Wensleydale; Yallourn North; Yallourn Fruit Zone.

NEW SOUTH WALES: Vegetable Creek.

QUEENSLAND: Mt. Tamborine.

Affinity.—Unknown.

Myrtaceidites parvus forma *anesus* forma nov.

Plate 1, Figs. 27, 28

Grains 9-14 μ in equatorial diameter, arci present; polar islands absent; exine smooth or faintly and indistinctly patterned.

Known range.—Eocene to Pliocene.

WESTERN AUSTRALIA: Hay-Denmark railway, 8662/1; Nornalup 32982.

SOUTH AUSTRALIA: Comaum, 619 ft 6 in.; Pidinga, 11-16 ft, 35 ft 6 in.-41 ft 6 in.

VICTORIA: Anglesea; Bambra, 106-110 ft; Nelson bore, 992 ft; Wensleydale.

NEW GUINEA: Era River.

Affinity.—Unknown.

(*d*) *Olacaceae*

Plate 1, Figs. 47-63

Fossil pollen grains which are morphologically identical with the apparently unique pollen type that characterizes the 2 olacaceous genera *Anacolosa* and *Cathedra* (Erdtman 1952) have been observed in residues of certain Tertiary deposits in the Otway Peninsula, south-west of Melbourne, and in South Australia. While in fundamental agreement with the pollen grains of both genera the fossils bear a greater resemblance to the pollen grains of *Anacolosa,* which are larger, thicker-walled, and less rounded than those of the species of *Cathedra* examined, *C. grandiflora* excepted (Appendix I). The present geographic distribution of the 2 genera (*Anacolosa*—India to the western Pacific islands, including New Guinea; *Cathedra*—Brazil) further supports a connection with *Anacolosa.*

Two sporomorphs can be distinguished on shape, size, and coarseness of sculpture. The smaller of the 2 is closely similar to the pollen of certain species of *Anacolosa* and appears to have been closely related to that genus. The larger has not as yet been matched with pollen of a living species.

Anacolosoid pollen grains have not previously been recorded as fossils; it is therefore proposed to erect a new sporotype to be known as *Anacolosidites* for the inclusion of such forms.

Anacolosidites n. spt.

Grains isopolar, medium to small, triangular to round-triangular in polar view, 6-porate, 3 pores towards the angles of each face. Sculpture indistinct to prominent.

Anacolosidites luteoides n. spm.

Plate 1, Figs. 47-50

Grains small, subtriangular in polar view with straight to slightly concave sides; equatorial diameter 19-24 μ. Pores usually close to the angles. Exine 1.5-2.5 μ; sexine as thick as nexine; sculpture ill-defined, ?finely reticulate.

Known range.—Eocene.

Occurrence.—A rare type occurring in very small numbers—most frequent at Birregurra, Vic.

VICTORIA: Anglesea; Birregurra, 760-898 ft; Gellibrand River; Dilwyn Clay.
SOUTH AUSTRALIA: Canopus Station, bore 1 at 900-910 ft.

Affinity.—Before the close relationships of *Anacolosidites luteoides* can be considered some supplementary details regarding the pollen of living species of *Anacolosa* require mention. In 1952, Erdtman noted that the position of the pores in relation to the poles varied in the 2 species he examined, being nearer to the poles in *A. griffithsii* Mast. than in *A. lutea* Gillespie. Further examples with pores in both positions have been encountered during the present investigation and although this difference is not always as clearly defined as it is in *A. griffithsii* and *A. lutea* the following approximate grouping on this character is possible:

(i) Species with pores near the poles (Plate 1, Figs. 51-53, 56, 57, 59): *A. arborea* K. & V. (Java, W. Bruck 3840, 13 by 23-26 μ); *A.*

densiflora Bedd. (Madras; Beddome s.n. 1861 ex Herb. Kew, equatorial diameter 20-24 μ); *A. griffithsii* (Tenasserim and Andamans; Helfer 821, in Erdtman 1952, p. 294, 14.5 by 23 μ); *A. ilicioides* Mast. (Siam; No. 1192, Herb. Kew, 12-14 by 24-29 μ); *A. luzonensis* Merr. (Panay, Philippine Is. Bureau of Sci., Manila, 35583, 15 by 21-26 μ); *A. multiflora* Merr. (Luzon, Philippine Is. Bureau of Sci., Manila 1417, 13-15 by 23-26 μ).

(ii) Species with pores near the angles (Plate 1, Figs. 54, 55, 58): *A. frutescens* Blume (Java, Bachen, 22521, 15-16 by 22-27 μ); *A. lutea* (Fiji, Erdtman 1952, p. 294, 14.5 by 23 μ); *A. papuana* Schellen (Guadalcanal; Kajewski 2466, 13-16 by 21-23 μ).

The sporomorph *Anacolosidites luteoides* almost certainly represents an Early Tertiary species of *Anacolosa* having affinities with *A. lutea* of Fiji and *A. papuana* of New Guinea and the adjacent islands. It is close to the pollen of both species in size, shape, the peripheral position of the pores, and the inconspicuous sculpture of the exine.

The genus *Anacolosa* is not represented in the present flora of Australia, its main development being in the tropical zone of the Western Pacific region and southern India. The occurrence of pollen grains of a probable Eocene species in Victorian deposits therefore provides another example of a living type that during the Tertiary period probably had a more extended southerly distribution (Cookson 1953).

Anacolosidites acutullus n. spm.

Plate 1, Figs. 62, 63

Grains medium, triangular in polar view with straight or slightly convex sides and acute angles; equatorial diameter 42 μ; pores close to the angles. Exine 2-3 μ, sexine slightly thinner than the nexine, rugulate, more finely so towards the angles.

Known range.—Eocene.

Occurrence.—A very rare type, seen at 4 Victorian localities: Anglesea; Birregurra; Castle Cove; Wensleydale.

Affinity.—This sporomorph is larger and has more acute angles and more distinct sculpture than the pollen of any of the living species of *Anacolosa* examined. However, its general anacolosoid form is highly suggestive of an affinity with *Anacolosa* or an allied extinct type.

(*e*) *?Proteaceae*

Plate 2, Figs. 64-66

Proteacidites pachypolus n. spm.

Plate 2, Figs. 64-66

Grains iso- or slightly sub-isopolar, 3- (rarely 4-) aperturate, oblate, triangular in polar view, 25-40 by *c.* 22 μ, with straight or concave sides, and a more or less prominent circular thickening (5-16 μ dia.), the size and projection of which vary in individual examples, at one or both of the poles. When both polar thickenings are present, one may be more strongly developed than the other. Exine about 2 μ (about 6 μ in the region of the polar thickenings), curving in slightly but not narrowing towards the apertures. Sexine about as thick as nexine, finely reticulate.

Known range.—Eocene to ?Oligocene. A rare type.

WESTERN AUSTRALIA: Hay-Denmark railway, 8662/1.

SOUTH AUSTRALIA: Canopus Station, 860-925 ft; Cootabarlow, 515-537 ft; Pidinga, 11-16 and 26 ft.

VICTORIA: Anglesea; Birregurra between 760 and 960 ft; Castle Cove; Nelson bore, 992 ft.

NEW SOUTH WALES: Vegetable Creek.

Affinity.—The sporomorph *Proteacidites pachypolus* cannot be identified with any living or fossil species. It has been associated with the sporotype *Proteacidites* on account of its general similarity to *Proteacidites adenanthoides,* an Australian Tertiary sporomorph morphologically close to the pollen of the living proteaceous species *Adenanthos barbigera* Lindl. However, the 2 forms can be readily distinguished from one another by the characteristic development in *P. pachypolus* of the clearly circumscribed polar thickenings.

(*f*) *Santalaceae*

Plate 2, Figs. 67-72

Santalumidites n. spt.

Grains approximating to those of living species of *Santalum,* 3-porate, prolate, with a broad oroid zone in which the exine is more coarsely sculptured and thicker than at the poles, the maximum thickness being around the pores.

Santalumidites cainozoicus n. spm.

Plate 2, Figs. 67-71

As for sporotype, 18-37 by 29-54 μ. Pores rounded to somewhat quadrangular; pattern obscure, ?rugulate.

Known range.—Lower Tertiary in Australia; Pliocene in New Guinea.

WESTERN AUSTRALIA: Hay-Denmark railway, 8662/9.

SOUTH AUSTRALIA: Canopus Station, 860-900 ft; Pidinga, 11-16 ft.

VICTORIA: Anglesea; Birregurra, 760-890 ft; Castle Cove, Nelson bore, 992 ft.

NEW SOUTH WALES: Vegetable Creek.

NEW GUINEA: Shu Creek.

Affinity.—While the grains comprising *S. cainozoicus* agree closely with the pollen grains of *Santalum,* they are considerably larger than those of the living Australian species that have been available for examination (Appendix I). However, the approximation of their size to that given by Selling (1947) for pollen of the Hawaiian species *S. freycinetianum* supports an affinity with *Santalum*. The "band-like thickenings of the exine (= arci)" observed by Selling in the pollen grains of the Hawaiian species and which are clearly defined in those of most of the living Australian species, have not been evident in the fossils.

The wide variation in size and coarseness of sculpture of the grains included in *Santalumidites cainozoicus*, a variation considerably greater than that known for pollen of any living species of *Santalum*, suggests that this sporomorph as here defined represents more than one Tertiary species. However, the number of individual examples of *S. cainozoicus* has been too small to permit a more detailed treatment.

The only other known occurrence of fossil *Santalum* pollen is the one reported by Selling (1947) in Quaternary deposits in Hawaii.

(*g*) *Sapindaceae*

Plate 2, Figs. 73-91

As previously mentioned by us (Section III (*c*)) and also by Selling (1947, p. 222) and Erdtman (1952, p. 397), pollen grains of some members of the Sapindaceae such, for example, as certain species of the tribe Cupanieae, which have triangular ambs and well-defined arci, are remarkably similar to those of the Myrtaceae. However, on the whole, the apertures of myrtaceous grains are broader and more pronounced than they are in the equivalent grains of the Cupanieae, and in addition most of the latter have a more or less well-defined sexinous reticulum, a type of sculpture rarely if ever evident in the pollen grains of the Myrtaceae.

Certain fossil pollen grains occur in Australian deposits which, on the basis of the characters just mentioned, seem more correctly placed in the Sapindaceae than in the Myrtaceae. All can be fairly closely matched with pollen grains of living Australian members of the Cupanieae and it seems reasonable to suppose that the fossils in question had some connection with this tribe. Since, however, the distinction between the pollen grains of individual living genera is not always sharply defined (see Table 2), it is proposed that fossil pollen grains with apparent cupanieaceous characters should be referred to the sporotype *Cupanieidites*, defined below, rather than connected with individual living genera.

Cupanieidites n. spt.

Grains medium-sized, tricolporate; amb triangular to almost circular, angulaperturate; arci present, either uniting to form more or less distinct polar islands or not reaching the poles. Sexine as thick as nexine, distinctly to faintly reticulate.

TABLE 2

MORPHOLOGICAL CHARACTERS OF THE POLLEN GRAINS OF SOME AUSTRALIAN MEMBERS OF THE TRIBE CUPANIEAE OF THE FAMILY SAPINDACEAE

Species	Equatorial Diameter (μ)	Sides of Amb Straight*	Arci Reaching the Poles	Polar Islands		Sexinous Reticulum Clear
				Present	Large	
Arytera foveolata F. Muell. (Isis Scrub, N.S.W., ex Herb. Syd.)	18-22	—	+	+	—	+
Cupaniopsis anacardioides (A. Rich.) Radlk. (Coopernook, N.S.W., ex Melb. Univ. Herb.)	22-27	±	+	+	—	±
C. curvidens Radlk. (SE. New Guinea, ex Herb. Melb.)	25-27	—	+	+	+	+
C. flagelliformis (Bail.) Radlk. (Capricornia, Qld., ex Herb. Melb.)	25-29	—	—	—	—	+
C. foveolata (F. Muell.) Radlk. (Rockingham Bay, Qld., ex Herb. Melb.)	20-25	±	±	±	—	+
C. fruticosa Radlk. (New Caledonia, ex Herb. Melb.)	18-24	—	+	+	—	+
C. serrata (F. Muell.) Radlk. (Rockingham Bay, Qld., ex Herb. Melb.)	20-30	±	—	—	—	+
C. shirleyana (Bail.) Radlk. (Bundaberg, ex Herb. Syd. No. 22424)	25-29	+	+	∓	—	+
C. wadsworthii (F. Muell.) Radlk. (Wide Bay, Qld., ex Herb. Melb.)	27-30	+	+	+	—	+
Diploglottis campbellii Cheel. (Tweed R., N.S.W., ex Herb. Syd. 11424)	18-21	+	+	+	—	—
D. cunninghamii Benth. (Clarence R., N.S.W., ex Herb. Melb.)	20-25	+	+	±	—	—
D. diphyllostegia (F. Muell.) Bail. (Rockingham Bay, Qld., ex Herb. Syd.)	18-23	+	+	±	—	—
Elattostachys bidwillii (Benth.) Radlk. (Qld. leg. Gay No. 163, ex Herb. Melb.)	22-25	—	+	+	+	—
E. nervosa (F. Muell.) Radlk. (E. Aust. leg. Leichhardt, ex Herb. Melb.)	27-28	—	+	+	+	—
E. xylocarpa (Cunn.) Radlk. (Nearkool Ck., Qld., ex Herb. Melb.)	23-27	—	+	+	+	—
Guioa acutifolia (F. Muell.) Radlk. (Cairns, Qld., ex Herb. Syd. 22438)	20-23	+	+	±	—	—

TABLE 2 (*Continued*)

Species	Equatorial Diameter (μ)	Sides of Amb Straight*	Arci Reaching the Poles	Polar Islands Present	Polar Islands Large	Sexinous Reticulum Clear
G. falcata Radlk. (Luzon, ex Herb. Syd.)	20-25	–	+	±	–	–
G. semiglauca (F. Muell.) Radlk. (Upper Allyn, N.S.W., ex Melb. Univ. Herb.)	18-20	–	+	±	–	–
Jagera pseudorhus (A. Rich.) Radlk. (Clarence R., N.S.W., ex Herb. Melb.)	23-29	–	+	∓	∓	+
Lepiderema punctulata (F. Muell.) Radlk. (Tweed R., N.S.W., ex Herb. Syd.)	23-26	±	+	+	–	+
Mischocarpus anodontus (F. Muell.) Radlk. (Hunter R., N.S.W., ex Herb. Melb.)	20-24	+	+	+	–	–
M. exangulatus (F. Muell.) Radlk. (Rockingham Bay, Qld., ex Herb. Syd.)	21-23	+	+	+	–	∓
M. pyriformis (F. Müll.) Radlk. (Urunga, N.S.W., ex Herb. Syd.)	20-25	+	+	∓	–	+
Rhysotoechia bifoliolata (F. Muell.) Radlk. (Myall Lakes, N.S.W., ex Herb. Syd.)	23-28	+	+	+	+	–
R. robertsonii (F. Muell.) Radlk. (Rockingham Bay, Qld., ex Herb. Syd.)	19-23	+	+	+	–	–
Sarcopteryx martyana (F. Muell.) Radlk. (Innisfail, Qld., ex Herb. Syd.)	16-24	+	+	±	–	±
S. stipitata (F. Muell.) Radlk. (Atherton Tableland, Qld., ex Herb. Melb.)	21-26	+	+	∓	–	+
Synima cordierii (F. Muell.) Radlk. (Daintree R., Qld., ex Herb. Syd.)	23-26	+	+	∓	–	–
Toechima dasyrrhache Radlk. (N.S.W., ex Herb. Syd.)	23-26	+	+	+	–	+
T. erythrocarpa (F. Muell.) Radlk. (Rockingham Bay, Qld., ex Herb. Syd.)	21-26	±	+	+	–	+
T. lanceolatum C. T. White (Atherton Tableland, Qld., ex Herb. Syd.)	18-23	+	+	∓	–	∓
T. tenax (Benth.) Radlk. (Moreton Bay, Qld., ex Herb. Melb.)	18-25	+	+	+	–	–

* The alternative character is "sides of amb convex".

Cupanieidites orthoteichus n. spm.

Plate 2, Figs. 73-78

Grains isopolar to subisopolar; amb sharply triangular with straight sides; arci prominent, forming distinct polar islands, equatorial diameter 20-30 μ. Sexine reticulate, mesh fine, sometimes indistinct.

Known range.—Eocene to Pliocene.

WESTERN AUSTRALIA: Hay-Denmark railway, 8662/1, 8662/9.

SOUTH AUSTRALIA: Canopus, 860-881 ft; Cootabarlow, 515-537 ft; Pidinga, 11-16 ft, 26 ft.

VICTORIA: Anglesea; Birregurra 760-761 ft; Castle Cove; Coode I.; Eastern View; Lal Lal B.51, 398 ft; Maryvale B.155, 552 ft; Nelson bore, 992 ft; Point Ronald; Wensleydale; Yallourn.

NEW SOUTH WALES: Vegetable Creek.

QUEENSLAND: Mt. Tamborine.

Affinity.—While the shape of the amb and the enclosure by the arci of relatively large polar islands are constant features of the grains included in *Cupanieidites orthoteichus,* the size of the mesh of the sexinous reticulum is a variable feature, in some cases being so small as to be almost imperceptible. It seems probable therefore that *C. orthoteichus,* as at present interpreted, represents more than one species.

Amongst the pollen grains of the living species examined, those of *Mischocarpus pyriformis* (F. Muell.) Radlk. (Plate 2, Fig. 79), a Queensland rain-forest tree, probably come nearest to *C. orthoteichus,* others approaching it being those of *Cupaniopsis curvidens* Radlk. (Plate 2, Fig. 80), *Jagera pseudorhus* (A. Rich.) Radlk. (Plate 2, Fig. 82), *Rhysotoechia bifoliolata* (F. Muell.) Radlk. (Plate 2, Fig. 81) and *Toechima tenax* (Benth.) Radlk.

Comments.—The occurrence of *C. orthoteichus* in Western Australia, South Australia, and Victoria during the Early Tertiary period shows that at that time the tribe Cupanieae must have had a wider distribution than at present. This tribe now has its greatest Australian development in the rain-forest areas of Queensland and extends southwards to about the latitude of Sydney.

Cupanieidites major n. spm.

Plate 2, Figs. 83-85

Grains isopolar; amb triangular with slightly convex sides, polar islands very small, equatorial diameter 29-34 μ. Sexinous reticulum fine and shallow.

Known range.—Eocene.

VICTORIA: Anglesea; Birregurra, 760-890 ft.

Affinity.—In the size and shape of the amb *Cupanieidites major* more closely approaches pollen grains of *Cupaniopsis wadsworthii* (F. Muell.) Radlk., a rain-forest tree of Queensland and New South Wales, than those of the other species examined, but differs in having a finer and shallower sexinous reticulum. The specimen shown in Plate 2, Figure 85, the only one of its kind isolated from a Pliocene deposit at Shu Creek, Papua, is provisionally included in *C. major.*

Cupanieidites reticularis n. spm.

Plate 2, Figs. 87-89

Grains isopolar; amb triangular with slightly convex sides; arci, which may or may not enclose polar islands, prominent; equatorial diameter 21-26 μ. Sexine reticulate, mesh clearly defined, small and relatively deep.

Known range.—Eocene.

VICTORIA: Anglesea; Birregurra, 842-843 ft.

Affinity.—This is a rare type which in the shape of the amb and type of sexinous reticulum is rather similar to pollen grains of *Lepiderema punctulata* (F. Muell.) Radlk. (Plate 2, Fig. 91) and *Sarcopteryx stipitata* (F. Muell.) Radlk. (Plate 2, Fig. 90). Considerably more examples will be needed before the more exact limits and affinity of *C. reticularis* can be determined.

(*h*) *Dicotyledonae—Incertae Sedis*

Plate 2, Figs. 92-99, 101-107

Tricolpites thomasii n. spm.*

Plate 2, Figs. 92-94

Grains triangular in polar view with straight to slightly concave sides, tricolpate, angulaperturate; equatorial diameter 23-31 μ. Exine deeply reticulate in the mesocolpia, almost smooth in the polar and apertural regions.

Known range.—Eocene.

SOUTH AUSTRALIA: Canopus B.1.
VICTORIA: Anglesea; Birregurra, 842-843 ft; Castle Cove.
NEW SOUTH WALES: Vegetable Creek.

Comments.—A very rare type, the affinity of which has not been determined. It shows some resemblance to certain members of the Loranthaceae.

Triorites edwardsii n. spm.*

Plate 2, Figs. 101-107

Grains flattened, triangular (rarely quadrangular) in polar view with more or less concave sides, angulaperturate, the apertures sunken and surrounded by an exinous rim of variable thickness and depth; equatorial diameter 18-49 μ. Exine 3-layered, 1.5-4.5 μ between the apertures. Sexine thin, finely and indistinctly patterned; nexine thicker than the sexine, especially where it overarches the apertures. In some examples (Plate 2, Figs. 101, 106) 2 superimposed "collars", partially separated by a minute space, surround a relatively deep extra-apertural cavity.

---

* The specific names have been given in appreciation of the interest taken in our work by Dr. D. E. Thomas, Mines Department of Victoria, and Dr. A. B. Edwards, Mineragraphic Section, C.S.I.R.O.

Known range.—?Paleocene to Lower Eocene.

SOUTH AUSTRALIA: Comaum at 619 ft 6 in. (1 example).

VICTORIA: Benwerrin; Birregurra, 1006-1020 ft; Eastern View; Lal Lal bore 51, 398 ft, bore 47, 216-223 ft; Nelson bore at 3723, 3874, and 4025 ft; Pebble Point.

Affinity.—Obscure. In the sunken apertures, the development in some examples of well-defined extra-apertural cavities, and the relative prominence of the nexine, *Triorites edwardsii* approaches the distinctive and as yet unclassified Australian sporomorph *Triorites magnificus* Cookson. However, the 2 forms are otherwise so distinct that a relationship between them seems unlikely.

Triorites edwardsii is a rare type with a limited known distribution in south-western Victoria and south-eastern South Australia. It appears to be restricted to the lowest horizon of the Lower Tertiary.

Triorites harrisii Couper

Plate 2, Figs. 95-99

This is one of the most abundant and widespread of the Australian Tertiary pollen types. The grains comprising it are medium-sized, angulaperturate, with a subtriangular to subspherical amb, the equatorial diameter of which ranges from 26 to 50 μ. The sexine is thicker than the nexine and distinctly patterned.

The Australian examples agree exactly with the description and figure of *T. harrisii* (Couper 1953), a commonly occurring pollen type in the Lower Eocene to Upper Miocene deposits of New Zealand, and there can be little doubt that they represent the same Tertiary species. Couper's suggestion that this was a wind-pollinated type is supported by the abundance of *T. harrisii* in Australian deposits.

Known range in Australia.—Eocene to Pliocene.

WESTERN AUSTRALIA: Hay-Denmark railway, 8662/1, 8662/9.

SOUTH AUSTRALIA: Canopus Station at 881-898 ft; Comaum, 619 ft; Cootabarlow at 515-537 ft; Moorlands; Pidinga at 11-16 ft, 35 ft 6 in.-41 ft 6 in.

VICTORIA: Anglesea; Bacchus Marsh; Balcombe Bay; Birregurra; Hamilton; Latrobe Valley; Nelson bore at 992 ft; Stony Creek; Wensleydale.

TASMANIA: Ouse River; Trevallyn.

NEW SOUTH WALES: Kiandra; Vegetable Creek.

QUEENSLAND: Mt. Tamborine; Stradbroke I.

NEW GUINEA: Orloli Region; Shu Creek.

Affinity.—Couper (1953) has already mentioned that a close similarity exists between *T. harrisii* and pollen of *Casuarina* and *Geniostoma rupestre* Forst. However, the pollen grains of *G. rupestre* are distinctly smaller and those of *Casuarina* usually both smaller and more aspidate than the grains comprising *T. harrisii.*

A close agreement, possibly indicative of definite affinity, also exists between *T. harrisii* and the pollen of the New Caledonian species *Canacomyrica monticola,* the 2 being practically indistinguishable from one another. Both have a comparable size range, average diameter, type of aperture, and exinous structure.

Canacomyrica is a southern representative of the family Myricaceae, known only from New Caledonia, and as such could quite likely have had a more southerly distribution during the Tertiary period. However, in the absence of confirmatory macroscopic material and until more is known of the pollen morphology of the Myricaceae as a whole, the affinity of *T. harrisii* with the Myricaceae in general, and *Canacomyrica monticola* in particular, cannot be established.

The occurrence of *T. harrisii* in Pliocene deposits of New Guinea is of interest.

IV. Acknowledgments

Pollen samples of living species were generously supplied by Sir Edward Salisbury, Royal Botanic Gardens, Kew; Dr. G. Taylor, British Museum, Natural History; Professor C. G. G. J. Van Steenis, Leiden, Holland; Dr. G. Erdtman, Bromma, Sweden; Dr. E. Boureau, Muséum National d'Histoire Naturelle, Paris; Mr. R. H. Anderson, Botanic Gardens, Sydney; Mr. A. W. Jessep, Botanic Gardens, Melbourne; Dr. B. J. Grieve, University of Western Australia; Mr. S. L. Everist, Botanic Gardens, Brisbane; and Miss C. M. Eardley, University of Adelaide.

Thanks are due to Mr. E. D. Gill, National Museum, Melbourne; Mr. G. Baker, Mineragraphic Investigations, C.S.I.R.O., Melbourne, and Mr. P. F. Morris and Mr. J. H. Willis, National Herbarium, Melbourne, for their helpful advice during the preparation of this paper.

The work was made possible by considerable financial assistance from the Commonwealth Scientific and Industrial Research Organization and the State Electricity Commission of Victoria.

V. References

Auer, V. (1933).—*Acta Geogr.* 5 (2): 1-313.
Baker, G. (1953).—Mem. Nat. Mus. Vict. No. 18: 125-34.
Bryan, W. H., and Jones, O. A. (1946).—*Univ. Qd. Pap.* 2 (12): 73.
Chapman, F. (1926).—*Proc. Roy. Soc. Vict.* 38: 183-91.
Cookson, Isabel C. (1953).—*Aust. J. Bot.* 1 (3): 462-72.
Cookson, Isabel C. (1954*a*).—*Aust. J. Bot.* 2 (1): 52-9.
Cookson, Isabel C. (1954*b*).—*Proc. Roy. Soc. Vict.* 66 (in press).

COULSON, A. (1950).—*Proc. Roy. Soc. Vict.* **60**: 157-62.

COUPER, R. A. (1953).—Paleont. Bull. N.Z. No. 22: 5-77.

ERDTMAN, G. (1943).—"An Introduction to Pollen Analysis." (Chronica Botanica Co.: U.S.A.)

ERDTMAN, G. (1952).—"Pollen Morphology and Plant Taxonomy—Angiosperms." (Almquist & Winsell: Stockholm.)

GARDNER, C. A. (1929).—W. Aust. Forest. Bull. No. 44: 5-10.

GILL, E. D. (1952).—*Aust. J. Sci.* **15** (2): 47-9.

GILL, E. D. (1953).—Mem. Nat. Mus. Vict. No. 18: 25-92.

MATTFELD, J. (1939).—*Bot. Jb.* **69**: 275-6.

PATERSON, HELEN T. (1935).—*Proc. Roy. Soc. Vict.* **48**: 67-74.

PATTON, R. T. (1936).—*Proc. Roy. Soc. Vict.* **49**: 36-9.

PIKE, KATHLEEN M. (1952).—*Proc. Roy. Soc. Vict.* **65** (1): 1-8.

RAGGATT, H. G., and CRESPIN, IRENE (1952).—*Aust. J. Sci.* **14**: 143-7.

SELLING, O. H. (1947).—Spec. Publ. Bishop Mus. No. 38.

SELLING, O. H. (1948).—Spec. Publ. Bishop Mus. No. 39.

SINGLETON, F. A. (1941).—*Proc. Roy. Soc. Vict.* **53** (1): 1-125.

THOMAS, D. E., and BARAGWANATH, W. (1949).—*Min. Geol. J. Vict.* **3**: 28-55.

WODEHOUSE, R. P. (1933).—*Bull. Torr. Bot. Cl.* **60**: 479-524.

APPENDIX I

Equatorial diameters of: *Casuarina cristata* Pritzel (Coolgardie Goldfield, W.A., ex Herb. Syd.) 24 (27) 29 μ; *C. decussata* Benth. (Merredin District, W.A., ex Herb. Syd.) 26 (30) 35 μ; *C. distyla* Vent. (Inland N.S.W.; Cambage 2689 ex Herb. Syd.) 23 (27) 31 μ, tetraploid (Strachan, Tas., ex Herb. Syd.) 31 (34) 36 μ; *C. fraseriana* Miq. (Perth, W.A., ex Herb. Syd.) 29 (33) 36 μ; *C. helmsii* Ewart & Gordon (Musgrave Range, S.A., ex Herb. Syd.) (Plate 1, Fig. 4) 32 μ; *C. humilis* Otto & Dietr. (Boya, N.S.W., ex Melb. Univ. Herb.) 26 (27) 29 μ; *C. inophloia* Muell. & Bailey (Warialda, N.S.W., ex Herb. Syd.) 26 (30) 36 μ; *C. microstachya* Miq. (W.A. leg. A. Drummond ex Herb. Syd.) 21 (25) 31 μ; *C. muelleriana* Miq. (Belair, S.A., ex Herb. Syd.) 31 (34) 36 μ; *C. nana* Sieb. ex Spreng. (Blue Mts., N.S.W., ex Melb. Univ. Herb.) 28 (31) 35 μ; *C. preissiana* Miq. (Albany, W.A., ex Herb. Syd.) 29 (30) 34 μ; *C. striata* E. D. Macklin. (Herb. Syd. No. 059) (Plate 1, Fig. 5) 26 (29) 35 μ; *C. stricta* Ait. (Cremorne, Tas., ex Melb. Univ. Herb.) (Plate 1, Fig. 6) 31 (34) 38 μ; *C. torulosa* Ait. (Tenterfield, N.S.W., ex Herb. Syd.) 29 (33) 36 μ.

Cathedra crassifolia Miers (Brazil; J. G. Kuhlmann 3053 in Erdtman 1952), 13.5 by 18 μ; *C. grandiflora* Loes. (Glazion 16712, Type ex Herb. Kew), 9-11 by 20-23 μ; *C. oblonga* Sleum (Brazil: A. Ducke 24964 ex Herb. Kew), 11-12 by 18 μ; *C. rubricaulis* Miers (Brazil, Lino Tatto, No. 3 ex Herb. Kew), 11-14 by 18-20 μ.

*Santalum acuminatum** (R. Br.) DC. (Nathalia, Vic., ex Herb. Vic.) 11-14 by 18-20 μ; *S. album* L. (ex Dehra Dun, India) 18-21 by 23-29 μ; *S. austrocaledonicum* Vieill. (Franc No. 2293 ex Herb. Qld.) 23-25 by 32-36 μ; *S. lanceolatum* R. Br. (NW. Aust. ex Melb. Univ. Herb.) 25-30 by 31-34 μ; *S. macgregori* F. Muell. (New Guinea ex Herb. Vic.) 20-25 by 27-32 μ; *S. obtusifolium* R. Br. (E. Aust. ex Herb. Vic.) 20-22 by 24-29 μ; *S. ovatum* R. Br. (Darwin ex Herb. Vic.) 15-20 by 20-23 μ. *S. persicarium** F. Muell. (NW. Vic. ex Melb. Univ. Herb.) 18-21 by 18-23 μ; *S. pilgeri* Rock. (Hawaii, Herb. Syd. 25578) 20-26 by 26-36 μ; *S. spicatum* (R. Br.) DC. (W. Aust. leg. J. Drummond ex Herb. Vic.) 11-14 by 16-19 μ; *S. yasi* Seem (Fiji, ex Herb. Vic.) 18-23 by 23-27 μ.

* Following Gardner (1929) these species have been included under *Santalum*.

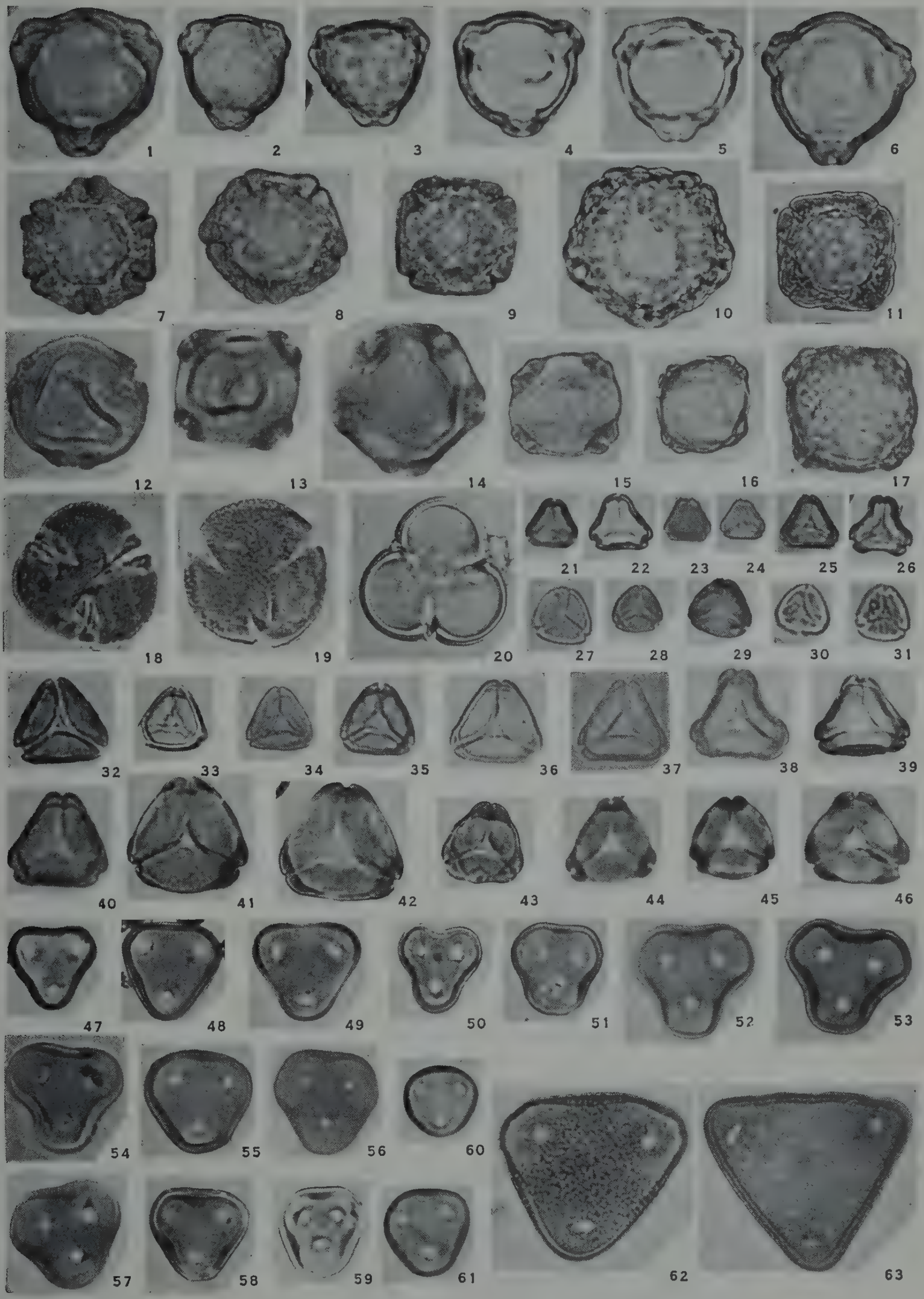
EXPLANATION OF PLATES 1 AND 2

All the photographs are from untouched negatives; all except the one shown in Figure 106 were taken at a magnification of 600 diameters.

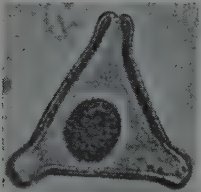
PLATE 1

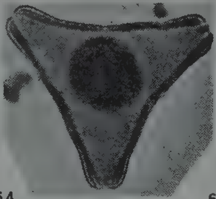
Fig. 1.—*Casuarinidites cainozoicus.* Stradbroke I., Qld.
Fig. 2.—*C. cainozoicus.* Denmark, W.A. No. 4487.
Fig. 3.—*C. cainozoicus.* Yallourn Open Cut, Vic.
Fig. 4.—*Casuarina helmsii.* Musgrave Range, S.A.
Fig. 5.—*C. striata.* South Australia.
Fig. 6.—*C. stricta.* Cremorne, Tas.
Figs. 7-9.—*Haloragacidites haloragoides.* Shannon River lignite, W.A.
Fig. 10.—*Haloragis salsoides*, five-pored grain. Maroubra, N.S.W.
Fig. 11.—*H. meziana*, four-pored grain. Grampians Mts., Vic.
Figs. 12-14.—*Haloragacidites myriophylloides*, three-, four-, and five-pored grains. Shu Creek, Papua.
Fig. 15.—*H. myriophylloides*, four-pored grain. Orloli Region, Papua.
Fig. 16.—*Myriophyllum verrucosum.* Mt. Surprise, Qld.
Fig. 17.—*M. longibracteolatum.* Bulahdelah, N.S.W.
Fig. 18.—*Gunnerites reticulatus.* Kerguelen Archipelago.
Fig. 19.—*G. reticulatus.* Orloli Region (512), Papua.
Fig. 20.—*Gunnera cordifolia.* Great Lake, Tas.
Fig. 21.—*Myrtaceidites eugeniioides.* Cootabarlow, S.A.
Fig. 22.—*M. eugeniioides.* Comaum, S.A.
Fig. 23.—*M. eugeniioides.* Yallourn, Vic.
Figs. 24-26.—*M. eugeniioides.* Wensleydale, Vic.
Fig. 27.—*M. parvus* forma *anesus.* Western Australia 8662/1.
Fig. 28.—*M. parvus* forma *anesus.* Anglesea, Vic.
Fig. 29.—*M. parvus* forma *nesus.* Anglesea, Vic.
Fig. 30.—*M. parvus* forma *nesus.* Mt. Tamborine, Qld.
Fig. 31.—*M. parvus* forma *nesus.* Yallourn North, Vic.
Fig. 32.—*M. mesonesus.* Anglesea, Vic.
Fig. 33.—*M. mesonesus.* Yallourn, Vic.
Fig. 34.—*M. mesonesus.* Shu Creek, Papua.
Figs. 35, 36.—*M. mesonesus.* Maryvale, Vic.
Fig. 37.—*Eucalyptus tessellaris.*
Fig. 38.—*Myrtaceidites eucalyptoides* forma *orthus.* Brookes Inlet, W.A.
Fig. 39.—*M. eucalyptoides* forma *orthus.* Stony Creek, Vic.
Fig. 40.—*M. eucalyptoides* forma *orthus.* Stradbroke I., Qld.
Fig. 41.—*M. eucalyptoides* forma *convexus.* Stradbroke I., Qld.
Figs. 42, 43.—*M. eucalyptoides* forma *convexus.* Hamilton, Vic.
Fig. 44.—*M. eucalyptoides* forma *convexus.* Smithton, Tas.
Fig. 45.—*M. eucalyptoides* forma *convexus.* Denmark, W.A.
Fig. 46.—*M. eucalyptoides* forma *convexus.* Shannon R., W.A.
Figs. 47, 48.—*Anacolosidites luteoides.* Anglesea, Vic.
Fig. 49.—*A. luteoides.* Birregurra, Vic.
Fig. 50.—*A. luteoides.* Dilwyn Clay, Princetown, Vic.
Fig. 51.—*Anacolosa densiflora.* Madras.
Fig. 52.—*A. arborea.* Java.
Fig. 53.—*A. ilicioides.* Siam.
Fig. 54.—*A. frutescens.* Java.
Fig. 55.—*A. papuana.* Guadalcanal.
Fig. 56.—*A. luzonensis.* Philippine Is.

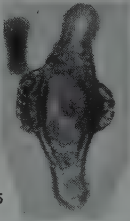
AUSTRALIAN CAINOZOIC DICOTYLEDON POLLEN

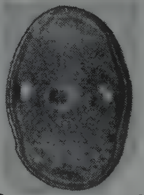

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
60
62
63
57
58
59
61

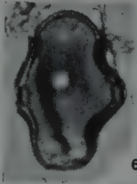
AUSTRALIAN CAINOZOIC DICOTYLEDON POLLEN

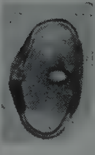

64

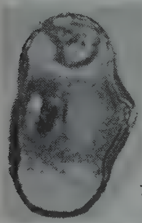

65

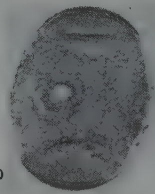

66

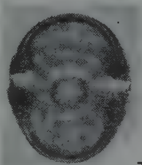

67

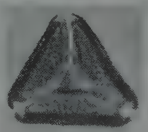

68

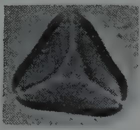

69

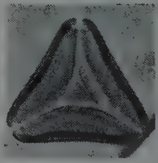

70

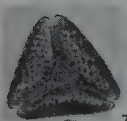

71

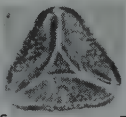

72

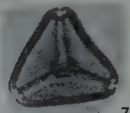

73

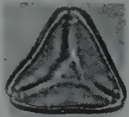

74

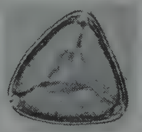

75

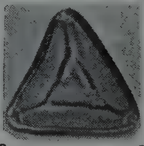

76

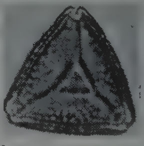

77

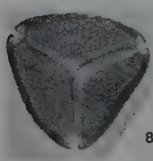

78

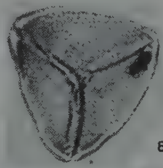

79

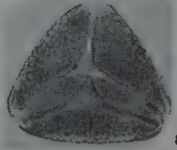

80

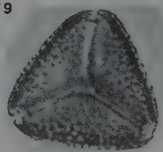

81

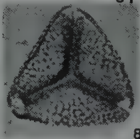

82

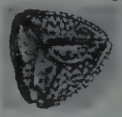

83

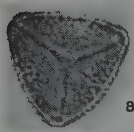

84

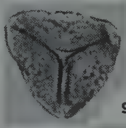

85

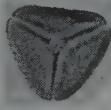

86

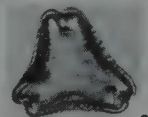

87

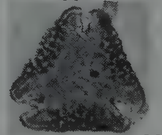

88

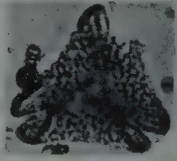

89

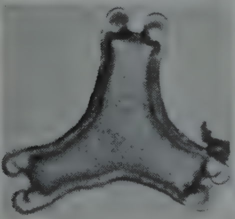

90

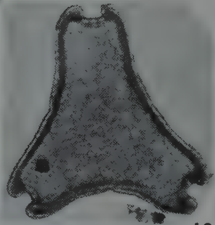

91

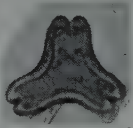

92

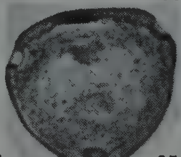

93

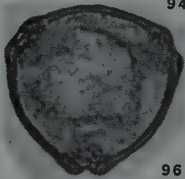

94

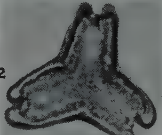

101

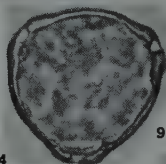

102

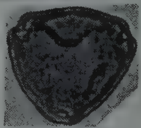

103

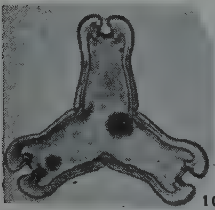

95

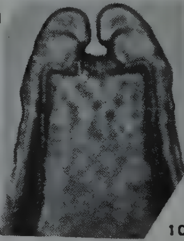

96

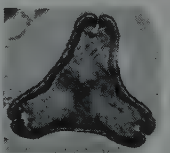

104

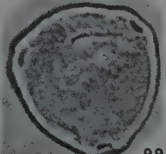

97


98


105


106


107


99

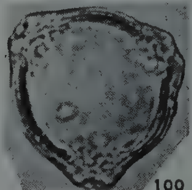

100

Fig. 57.—*A. multiflora.* Philippine Is.
Fig. 58.—*A. lutea.* Fiji.
Fig. 59.—*A. griffithsii.* Tenasserim and Andamans.
Fig. 60.—*Cathedra oblonga.* Brazil.
Fig. 61.—*C. rubricaulis.* Brazil.
Fig. 62.—*Anacolosidites acutulus.* Birregurra, Vic.
Fig. 63.—*A. acutulus.* Lal Lal, Vic. B.51, 398 ft.

PLATE 2

Fig. 64.—*Proteacidites pachypolus.* Canopus, S.A., 900-910 ft.
Fig. 65.—*P. pachypolus.* Pidinga, S.A.
Fig. 66.—*P. pachypolus.* Equatorial view of a grain from Anglesea, Vic.
Fig. 67.—*Santalumidites cainozoicus.* Canopus, S.A., 881-898 ft.
Fig. 68.—*S. cainozoicus.* Pidinga, S.A., 11-16 ft.
Fig. 69.—*S. cainozoicus.* Castle Cove, Vic.
Fig. 70.—*S. cainozoicus.* Birregurra, Vic.
Fig. 71.—*S. cainozoicus.* Shu Creek, Papua.
Fig. 72.—*Santalum lanceolatum.* West (26 miles) of Fitzroy Crossing, W.A.
Fig. 73.—*Cupanieidites orthoteichus.* Hay-Denmark railway, W.A., No. 8662/9.
Fig. 74.—*C. orthoteichus.* Yallourn Open Cut, Vic.
Fig. 75.—*C. orthoteichus.* Maryvale, Vic. B.155, 552 ft.
Fig. 76.—*C. orthoteichus.* Anglesea, Vic.
Fig. 77.—*C. orthoteichus.* Gellibrand River (Princetown Member), Vic.
Fig. 78.—*C. orthoteichus.* Canopus, S.A., 860-881 ft.
Fig. 79.—*Mischocarpus pyriformis.* Brisbane Range, Qld.
Fig. 80.—*Cupaniopsis curvidens.* SE. New Guinea.
Fig. 81.—*Rhysotoechia bifoliolata.* Myall Lakes, N.S.W.
Fig. 82.—*Jagera pseudorhus.* Clarence River, N.S.W.
Fig. 83.—*Cupanieidites major.* Anglesea, Vic.
Fig. 84.—*C. major.* Anglesea, Vic.
Fig. 85.—Cf. *C. major.* Shu Creek, Papua.
Fig. 86.—*Cupaniopsis wadsworthii.* Wide Bay, Qld.
Figs. 87, 88.—*Cupanieidites reticularis.* Birregurra, Vic., 842-843 ft.
Fig. 89.—*C. reticularis.* Anglesea, Vic.
Fig. 90.—*Sarcopteryx stipitata.* Atherton Tableland, Qld.
Fig. 91.—*Lepiderema punctulata.* Tweed River, N.S.W.
Fig. 92.—*Tricolpites thomasii.* Birregurra, Vic.
Fig. 93.—*T. thomasii.* Anglesea, Vic.
Fig. 94.—*T. thomasii.* Castle Cove, Vic.
Fig. 95.—*Triorites harrisii.* Hamilton, Vic.
Fig. 96.—*T. harrisii.* Pidinga, S.A.
Fig. 97.—*T. harrisii.* Yallourn, Vic.
Fig. 98.—*T. harrisii.* Birregurra, Vic., 842-843 ft.
Fig. 99.—*T. harrisii.* Orloli Region, Papua.
Fig. 100.—*Canacomyrica monticola.* New Caledonia.
Figs. 101, 102.—*Triorites edwardsii.* Lal Lal, Vic. B.51, 398 ft.
Fig. 103.—*T. edwardsii.* Benwerrin, Vic.
Fig. 104.—*T. edwardsii.* Eastern View, Vic.
Fig. 105.—*T. edwardsii.* Pebble Point Formation, Vic.
Fig. 106.—*T. edwardsii.* Lal Lal, Vic. B.47, 216-223 ft. × 1350.
Fig. 107.—*T. edwardsii.* Birregurra, Vic. B.1, 1019-1020 ft.

THE ECOLOGY OF THE SOIL FUNGI OF AN AUSTRALIAN HEATHLAND

By ETHEL I. MCLENNAN* and SOPHIE C. DUCKER*

(*Manuscript received December* 15, 1953)

Summary

The distribution of microfungi in an Australian heathland soil has been investigated. Unlike the typical distribution for soil organisms, the numbers did not decrease progressively with depth, for the B horizon showed a comparable population both in numbers and types to that of the A_1 layer even at depths of 60 in. or more. This distribution is correlated with the organic carbon content of the ortstein layer.

The results obtained from the direct and indirect methods for determining the numbers of fungi per gram of soil were compared; from this comparison evidence was gained to support the statement that the suspension technique gives a fair picture of the soil population and does not reflect a high sporing capacity of a few fungi, as has been so often stated.

One hundred and seven species of fungi have been isolated from this soil. *Mortierella ramanniana* is the commonest fungus and it occurs right through the profile. The genus *Penicillium* with its multiplicity of species is the dominant genus.

Several species of *Aspergillus* appeared frequently on the plates and it is this genus which provides the forms that characterize this particular soil, including three new species of the genus. All the other fungi that were isolated have been recorded from northern hemisphere soils and are part of a cosmopolitan soil flora.

Ascosporic and sclerotial types characterize the litter fungi and those forms associated with plant parts in the soil, rather than the general fungal soil flora.

I. INTRODUCTION

Many fungi have been isolated from soil; Gilman and Abbott (1927) and Gilman (1945), bringing together the various records, listed 138 genera. This total includes representatives of most of the fungal groups, with the striking exception of the Basidiomycetes (Table 1).

Gilman gave an extensive bibliography, which indicates that the list is a comprehensive one at least for Great Britain, Europe, and North America. He included for the southern hemisphere the records of Dixon (1928, 1930), Dixon-Stewart (1932), and Cookson (1937). Jensen (1934) made no analysis of the composition of the fungal flora, but noted a few of the predominant forms. Although the Australian records are so few, yet they provide evidence to support the generalization that the soil fungal flora is a very uniform flora irrespective of types of soil or geographical position, at least so far as the genera that compose it are concerned (Burges 1939).

* Botany Department, University of Melbourne.

While the general nature of the soil flora has been recognized, very little is known about the ecology of the fungal population in Australian soils. Jensen studied the microflora of 50 New South Wales soils of different types in an attempt to relate the numbers of bacteria, Actinomycetes, and fungi with certain external factors, especially moisture and temperature. The soil samples he used were inadequately described and were not collected with any precision in relation to the soil profile, the majority were taken from the upper 10 cm of the soil. Jensen concluded as a result of his counts of microorganisms that there was a definite correlation between the content of organic matter and the numbers of bacteria, Actinomycetes, and fungi, that the soil reaction showed a significant correlation with the numbers of fungi though less marked than that with the organic matter, and that the moisture content of the soil did not show any definite influence on any of the groups, but several soils from dry districts were very poor in fungi. None of the groups showed any close correlation with temperature or seasonal changes.

TABLE 1

GROUPING OF KNOWN SOIL FUNGI

Group	Genera	Species
Phycomycetes	37	199
Ascomycetes	18	30
Basidiomycetes*	—	—
Fungi Imperfecti		
Sphaeropsidales	5	6
Melanconiales	1	1
Moniliales		
Moniliaceae	28	244 (includes 124 Penicillia)
Dematiaceae	31	68
Tuberculariaceae	8	55
Stilbaceae	8	9
Mycelia sterilia	2	2
	138	614

* *Rhizoctonia* included in Mycelia sterilia.

The actual distribution of organisms through the horizons of some soil profiles has been studied in Canada. Gray and McMaster (1933), examining the microbiological activity of virgin podzol soils in the province of Quebec, restricted their studies to the bacteria and Actinomycetes. Gray and Taylor (1935) extended this study to other podzol soils, one of which had a B horizon described by them as follows: "6″ red-brown sand, extending to below 12″, with 'ortstein' concretions fragmenting by hand pressure; organic matter and fibrous roots present".

This was overlain by an A_2 horizon of leached sand. From this description this podzol (sample VC) approximates in type to the soil studied in this paper. Although the organic carbon of the B horizon was greater than that of the A_2 (leached) it was much less in proportion to that of the A_1 than in the Australian podzol and shows a corresponding fall in the number of fungi from 487,000 per gram of soil in the A_1 to 5,580 per gram in the B horizon.

More recently Warcup (1951*a*), in a study of five English natural grassland soils, included one (sample E) with a B horizon of which "the uppermost 2.5″ is a dark purplish brown humus-iron pan. Portions of this project downwards as inverted cones with yellow stratified sand in between". The pH of this horizon was given as 4.6.

The present work was undertaken to investigate the ecology of the fungal population of a sandy podzolic soil which is found sporadically, but in extensive areas, in southern Victoria.

II. THE SOIL STUDIED

The soil has been described and mapped as Cranbourne sand (Leeper 1948). It is chemically poor in nutrients and carries a natural and very characteristic heath vegetation. The particular area under investigation is situated in the Frankston district, and the heathland is dominated by a few scattered clumps of *Eucalyptus viminalis* Labill. The area is covered by a stratum of low shrubs, most of which have a characteristic microphyllous and xeromorphic habit, the three most commonly occurring species being *Leptospermum myrsinoides* Schlech., *Lepidosperma concavum* R. Br., and *Hypolaena fastigiata* R. Br., with *Leucopogon virgatus* R. Br. and *Epacris impressa* Labill. next in order of frequency. Beneath the shrubs there is a sparse ground stratum of herbs. The old dunes at Frankston consist of sand which was wind-sorted during the late Pleistocene arid period. The soil has developed a podzolic profile and is characterized by the development of hard dark brown material known as ortstein or "coffee rock" which consists of sand cemented together largely by organic matter.

A typical profile may be described as follows:

A_0	Litter	A very sparse accumulation of undecomposed leaves and twigs.
A_1	0-22 in.	At 3 in. grey (N 5.5)*; moist, dark grey (5 Y 4/1), organic matter and roots abundant.
A_2	22-33 in.	At 27 in. white (N 8); moist, grey (5 Y 6/1); this is a leached layer with roots still abundant. At 33 in. a sudden transition to B.
B	33-36 in.	At 34 in. very dark brown (10 YR 2/21); moist, black (10 YR 2/1). This is the ortstein or "coffee-rock" with abundant organic matter and only a trace of iron.
B-C	36 in.+	At 46 in. brownish yellow (10 YR 6/8); moist yellowish brown (10 YR 5/6).

---

* Munsell Color Co. Inc. (1948).

The profile at C shows an even-textured sand with little to no organic matter, although roots extend into this horizon.

The general profile of this soil is further characterized by the downward extension of the "coffee-rock" for varying distances into the C horizon, in extreme cases beyond 12 ft. The extensions are in the form of "pipes" of the dark brown layer with a core of leached sand similar to that of the A_2 horizon (Plate 1).

If the A horizon is removed and the exposed coffee-rock is scraped carefully away to a point just below the horizon junction of the B and C layers, the surface shows an irregular pattern of patches of leached sand surrounded by the dark coffee-rock material (Plate 2). This photograph suggests the profuse development of these vertical extensions running into and through the lower horizon.

Analysis of this podzolic soil yields results which are typified by those shown in Table 2.

TABLE 2

RESULTS OF MECHANICAL AND PARTIAL CHEMICAL ANALYSES OF THE FRANKSTON SOIL

Horizon	A_1	A_2	B	C
Depth (in.)	0-18	18-34	34-38	38+
pH	4.6	5.2	4.8	5.2
Coarse sand (%)	86.1	86.4	86.0	92.6
Fine sand (%)	9.4	9.6	9.2	3.7
Silt (%)	1.6	0.6	1.5	0.5
Clay (%)	2.9	3.4	3.3	3.2
Organic carbon (%)	1.51	0.30	1.34	—
Water-holding capacity (%)	28.1	25.8	34.9	25.0

III. METHODS

Soil samples were collected at intervals throughout the year. They were taken from pits dug at various spots through the heathland and were obtained by inserting a sterile soil borer into the soil at the appropriate levels. The samples were transferred to sterile containers. Estimates of the number of fungi present in the various samples were made using both the plate-counting technique and the direct observational method (Jones and Mollison 1948). The plating method involves so many steps in procedure that unless care is taken there is a probability of serious error. To minimize this, the technique as outlined by James and Sutherland (1939*b*) was followed.

Six 25-g aliquots were taken from each of the samples to be tested and each was placed in sterile water to yield 1: 50 dilution. The flasks were thoroughly shaken and 1 ml was then transferred to each of three flasks containing 100 ml of sterile water, yielding 1: 5000 dilution.

From each of the three flasks, two 1-ml samples were plated out with agar (six replicate plates from each of the six original 25-g samples). It has been shown by James and Sutherland (1939*a*) that an analysis of variance indicated that there were significant differences in counts of fungi obtained by the more usual procedure where one 25-g sample was taken and several consecutive dilutions made from it, whatever the number of replicate plates poured from the final dilution (Brierley, Jewson, and Brierley 1927). The medium employed for the soil dilution plates was a malt peptone agar as used by Thom and Raper (1949). Its composition is:

Malt extract	20.0 g
Dextrose	20.0 g
Peptone	1.0 g
Agar	25.0 g
Distilled water	1.0 l.

The pH was 4.7.

The plates were incubated for 48 hr at 24°C and the colonies were then transferred to malt slopes. The plates were incubated for a further period and the slower-developing colonies were then subcultured as they appeared.

TABLE 3

RESULTS OBTAINED BY THE DIRECT COUNT METHOD APPLIED TO THE THREE HORIZONS OF THE PODZOL

Slides	Total No. of Pieces of Mycelium per 20 Fields Horizon			Total Length (μ) of Mycelium per 20 Fields Horizon			χ^2 of Total No. of Pieces of Mycelium per 20 Fields Horizon		
	A_1	B	C	A_1	B	C	A_1	B	C
1-3	30	13	6	272.5	117.0	37.0	16.65	22.38	20.66
4-6	33	10	6	377.5	114.5	27.5	21.98	26.0	20.37
7-9	34	12	4	326.5	143.5	33	14.29	14.66	15.4

The direct observational method as described by Jones and Mollison was followed exactly. The magnification was × 450. Many stains were tried but the counts were finally made using films stained with aniline blue as suggested in the original paper. Warcup's (1950) soil plates were also used during the course of this investigation.

IV. ESTIMATION OF FUNGAL POPULATIONS

(*a*) *Comparison of the Direct and Plate-counting Techniques*

The average number of viable fungal particles per gram of soil calculated by the plating method is indicated in Figure 1. A typical set of results obtained by the direct count method as applied to soil from the three horizons (A, B, and C) of the profile are set out in Table 3.

Estimates of the number of pieces of mycelium per gram of soil made by the direct count method give higher figures for the fungal population than those obtained by the plate-count technique (Table 4).

TABLE 4

COMPARISON OF THE NUMBERS OF VIABLE PARTICLES PER GRAM OF SOIL AS DETERMINED BY THE PLATING AND THE DIRECT COUNT TECHNIQUES

Horizon	Plate Count (Sept. 1948)	Direct Count (Sept. 1948)
A_1	76,500	165,048
B	32,000	91,262
C	7,500	29,126

It may be seen from Table 4 that the results from the direct method are from two to four times higher than those assessed by the plate counts. This lack of agreement between results from the two methods has been noted by Skinner, Jones, and Mollison (1952). There is little doubt that the discrepancy is mainly due to the difficulty in visually determining viable from non-viable mycelial fragments.

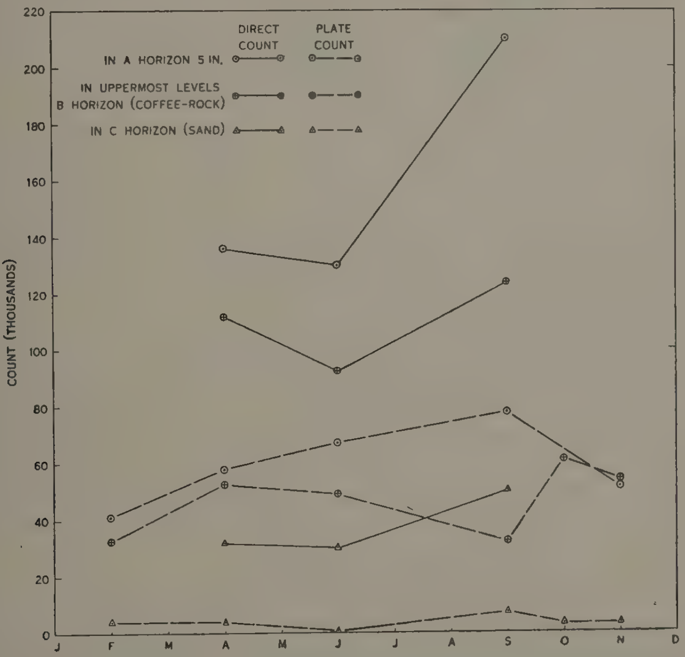


Fig. 1.—Average numbers of fungi in thousands per gram of soil through various months of the year obtained by the plate count method and by the direct count technique.

This two- to four-fold increase in fungal units per gram of soil given by the direct method gives vital support to the contention that fungi normally occur in soil in the mycelial condition (McLennan 1928) and that the plate counts are not a reflection of sporing capacity of the individual components of the population. If this were so, one could reasonably expect the higher count from the plating method, where spores, as well as mycelial fragments, could produce colonies rather than from the direct count *where only mycelial fragments are the units counted.* This conclusion was substantiated by microscopic examination of the soil slides. Although some observers have reported spores in preparations made by the direct method and figures of them have been published (Jones and Mollison 1948) in the many slides that have been made from the podzol and examined under magnifications up to × 1000 very few spores have been observed and they must occur certainly only rarely (see Plates 3 and 4).

Warcup (1951*a*) in commenting upon the high fungal counts for his acid grassland soils (*D* and *E*) stated they "were largely due to colonies of *Penicillium.* Microscopical examination of samples of *E* soil showed that many of these colonies developed from spores which were present in the soil. It would seem that in these acid grasslands a high number of colonies per gram may reflect a high sporing capacity of a few species of fungi rather than a high level of fungal activity in the soil."

He arrived at his figures for numbers per gram of soil by the dilution technique as set out by Waksman (1927). Unless Warcup estimated the number of fungal particles in the highly acid grassland soil by the direct method as outlined by Jones and Mollison (1948) and compared the results with those from the plate method one cannot accept his statement that high numbers reflect a high sporing capacity.

Skinner, Jones, and Mollison (1952), dealing with samples of Broadbalk soils at Rothamsted, found the greatest number of fungal particles in a plot receiving a dressing of complete minerals plus ammonium sulphate (plot 7). The direct counts were two to four times greater than that given by the plate counts. If the dressing had stimulated the sporing capacity of the soil fungi, we would expect the result to have been reversed.

(*b*) *Chesters' Immersion Tubes*

An attempt was made to isolate the soil fungi in situ using Chesters' (1940, 1948) immersion tubes. The very few genera isolated by this method had been repeatedly isolated by the plate technique.

The forms most frequently encountered represented the spreading mycelial types, e.g. *Trichoderma, Mortierella, Mucor,* and other *Phycomycetes.* The spiral capillaries of the immersion tubes are arranged over 1½ in. of tube length and offer very restricted entry to fungi in this area. The number and kind of types obtained in such tubes must compare unfavourably with the number and types recorded when a more representative soil sample is used, as in the dilution plating method, and as the technique necessitates the use of a culture medium in the tubes the criticism of the selectiveness of the plating method applies with equal force to this technique. Chesters stated that, using the immersion method, experiments showed that in cultivated and pasture soils the dominant fungi could be arranged in three series indicative of the relative frequency of the genera so isolated. He included the following fungi in each group:

TABLE 5

DOMINANCE OF MORTIERELLA RAMANNIANA OVER ALL OTHER FUNGI IN THE A AND B HORIZONS OF THE FRANKSTON PODZOL

Date	Horizon	Total Nos. of Colonies on 36 Plates	Nos. of Colonies of *M. ramanniana*	Percentage *M. ramanniana* Present
September 1946	A	744	677	91
	B	299	243	81
	C	67	21	31
October 1946	A	211	160	76
	B	256	236	92
	C	10	5	50
March 1947	A	570	559	98
	B	759	743	98
	C	17	7	41
April 1947	A	421	330	78
	B	859	814	95
	C	42	7	17
June 1947	A	474	387	82
	B	350	245	70
	C	14	2	14
October 1948	A	479	238	50
	B	448	357	80
	C	20	5	25

(1) *Mortierella, Mucor, Pythium.*
(2) *Rhizoctonia, Rhizopus, Zygorrhynchus, Fusarium.*
(3) *Cephalosporium, Circinella, Cunninghamella, Sordaria, Hyalopus, Botrytis, Phoma.*

All these genera with the exception of *Cephalosporium* and *Hyalopus* are known to us in culture and are all characterized by their quick-growing habit. Gilman and Abbot describe *Hyalopus* in culture as "turf extended" and some *Cephalosporium* spp. as "colonies spreading" so that this list includes only spreading growth forms. This method gives quite inadequate data for conclusions to be drawn about the soil fungal population. This fact is very well emphasized in Table 9 of Chesters' paper (1948) in which, from the core of soil removed to insert the immersion tube, he recorded 34 fungi isolated by the soil suspension method, including 24 species of *Penicillium,* and from the immersion tube at various levels only four fungi, two isolations of *Fusarium* sp. and two isolations of *Mucor hiemalis.*

The absence of these latter forms from the suspension plates in this experiment seems entirely fortuitous, for reference to his Table 7 shows again 35 isolations from the suspension technique and only seven by the immersion tube method, all of which were spreading forms (including *Mucor hiemalis*) and *all* were recorded from the suspension plates.

V. FREQUENCY AND DISTRIBUTION OF THE DOMINANT GENERA IN THE THREE HORIZONS OF THE PROFILE

(*a*) *General*

The outstanding feature of the dilution plates prepared from both the A and B horizons was the overwhelming dominance of *Mortierella ramanniana* (Table 5). This fungus is mainly responsible for aggregating the sandy soil together, for the slides made by the Jones and Mollison method showed numerous non-septate pieces of mycelia wrapping round the soil particles and, judging by the dominance of *M. ramanniana* on the agar plates, they must in the main belong to this form (Plates 3 and 4). It is interesting to note that Waksman (1922) described a species of *Zygorrhynchus* as being so abundant in the poor sandy soils of the Sassafras series of New Jersey that it held the sand together into compact masses. Martin and Anderson (1943) also reported that with a sandy loam soil *Mucor rouxi* proved to be a good soil binder.

TABLE 6

FREQUENCY OF DOMINANT GENERA EXPRESSED AS THE AVERAGE OF SEVEN SOIL DILUTION EXPERIMENTS

Horizon	*Mortierella ramanniana*	*Penicillium* spp.	*Aspergillus* spp.	Other Fungi	Totals
A	331	68	7	9	415
B	398	25	5	18	446
C	8	9	1	4	22

The genus *Penicillium* comes next in frequency on the plates and it is characterized by the *multiplicity of its species.* They extend right through the various horizons but a few occurred so recurrently and so abundantly that they might be classed as characteristic species; these are *P. adametzi, P. janthinellum, P. nigricans, P. restrictum,* and to a lesser extent *P. spinulosum.*

Aspergillus, with eight species, ranks as the next most representative genus, at least for the A and B horizons. It provides also two or three undescribed species which are exceptions to the general cosmopolitan nature of the fungal flora of this soil. One of these is more abundant than the other species and its distribution extends into the C horizon.

Table 6 represents the average number of colonies of each fungus appearing on 36 replicate plates for each of the seven experiments made at intervals throughout the year. The total number of colonies for horizons A and B are approximately equal; however, when the figures for any individual experiment are analysed this approximation does not always exist. Thrower (1954) has shown that the differences between the counts obtained at monthly intervals are not significantly greater than the differences among counts obtained from individual samples of soil collected from different places on the same day, so that the differences between the population of the soil at monthly intervals is probably due merely to variation between samples of soil. The average total figure derived from seven samplings is taken therefore to express the density of the population at the various levels of the profile. Excluding *Mortierella, Penicillium,* and *Aspergillus,* 37 genera (grouped together as "other fungi") were isolated from the soil, 15 extended through the three horizons.

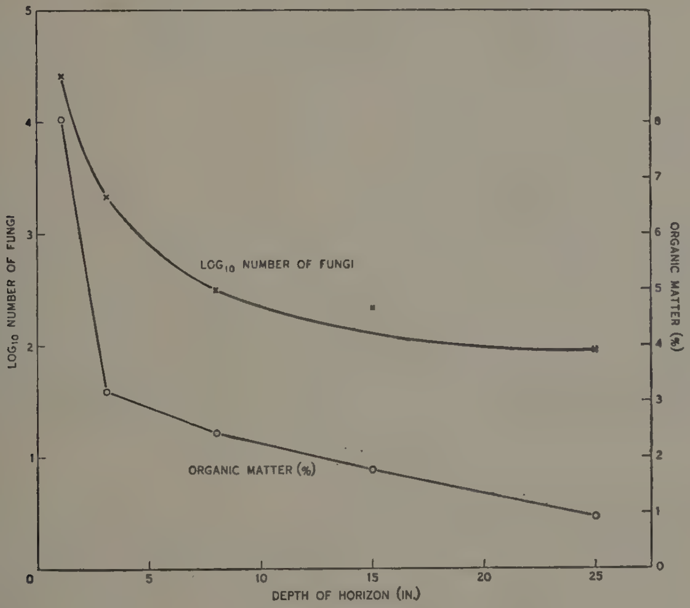


Fig. 2.—Fall in numbers of fungi per gram of soil as percentage of organic matter falls with increased depth.

(*b*) *Vertical Distribution of the Fungal Population in the Frankston Soil*

It is generally stated that there is a progressive and pronounced decrease in the number of fungal colonies that appear on plates as the soil samples are taken from increasing depths (Brierley, Jewson, and Brierley 1927; Brown and Benton 1930; Timonin 1938).

Figure 2 represents some results presented by Timonin and shows the fall in numbers of fungi through the successive levels of a soil profile. The distribution of the fungal population of the podzol under investigation does not fit into this general scheme.

TABLE 7

AVERAGE NUMBER OF FUNGAL COLONIES OBTAINED PER PLATE AT VARYING DEPTHS THROUGH THE PROFILE

Horizon	Depth (in.)	Sept. 1946	Oct. 1946	April 1947	June 1947	Oct. 1947	Average
A	8	6.4	2.9	5.8	6.5	6.6	5.6
B	32	5.3	3.5	11.9	4.8	6.1	6.3
C	42	0.9	0.13	0.5	0.19	0.27	0.4

Reference has often been made to the possibility of fungal spores being washed downwards through soil, particularly through sandy soil. Burges (1950) has shown that if spores possess waxy non-wetting coats there is very little movement vertically. The very rare occurrence of fungal spores in any of the direct count slides made from various soil levels lends support to his conclusion and suggests that the vertical distribution of fungi is a more or less stable phenomenon.

TABLE 8

PERCENTAGE MOISTURE AND CARBON CONTENTS OF THE A_2 AND B HORIZONS

Horizon	Sample	Depth (in.)	Moisture Content (%)	Carbon Content (expressed as loss on ignition)
A_2	1	16	4.9	0.9
A_2	2	16	5.6	0.8
A_2	3	16	4.8	0.6
A_2	4	24	4.5	0.2
B	1	32	5.8	3.7
B	2	32	8.0	1.8
B	3	32	13.8	5.3
B	Pipe 1	40	7.5	1.4
B	Pipe 2	40	5.1	1.9
B	Pipe 3	40	5.4	1.9
B	Pipe 4	40	8.2	2.4

Table 7 gives the average number of colonies occurring on plates when samples from the three horizons A, B, and C were analysed at intervals over several months of the year. If one excludes the high figure for B in the April count, the average number of colonies per plate is approximately equal in the A and B horizon.

(c) *The Ortstein Layer*

The B horizon is approximately 3-6 in. thick and is overlain by the A horizon which is of variable depth so that the ortstein occurs at different horizontal levels in the area, the average depth is about 32 in. It shows an interesting feature in the presence of pipe-like extensions projecting downwards into the underlying horizon. These "pipes" in cross section show an outer cylinder of ortstein with a central core of leached soil resembling the A_2 horizon (see Plates 1 and 2).

TABLE 9

NUMBERS OF PIECES OF MYCELIUM PER GRAM OF SOIL AT SUCCESSIVE LEVELS OF THE PODZOL

Horizon	No. of Pieces
A_1	3.8×10^5
A_2	1.2×10^5
B	2.1×10^5

The organic carbon content of the horizontal ortstein (approx. 32 in. from surface) is comparable to that of the A_1 horizon and as one samples vertically down the pipe the figure remains high, together with the soil water content, until the pipe starts to fade out, when the figures fall sharply. This increase in carbon content in the B horizon compared with that of the A_2 horizon is paralleled by an increase in the number of fungi (Table 9). Samples taken from the outer ortstein cylinder progressively down the pipes show that the numbers of fungi per gram of soil remain comparable with those for the horizontal layer until the lower ends of the pipe-like extensions are reached (Table 10).

TABLE 10

DISTRIBUTION OF FUNGI IN THE ORTSTEIN

Downward Extension of Ortstein Pipes (in.)	Nos. of Pieces of Mycelium per g Soil		
	"Pipe" 1	"Pipe" 2	"Pipe" 3
29-33	21,600	26,000	27,900
37	—	—	20,400
44	23,800	29,000	2,500
53	25,800	—	—
62	17,500	—	—
68	2,750	2,250	—

Timonin (1938) and Burges (1939) suggest that the most important factor governing the distribution of soil fungi is the distribution of organic matter, that this is so is evident from the results presented in Table 10.

When the pipe is short, e.g. "pipe" 3, the number of fungi per gram of soil falls at the 44-in. level to the number that characterizes the C horizon. When the organic content is carried deeper into the profile, as when the pipes are long (pipes 1 and 2), then at the 60-in. level, in the pipe cylinders, the numbers are strictly comparable to those at the 30 in.; the low numbers characteristic of the C horizon appeared at 68 in. when both pipes had petered out.

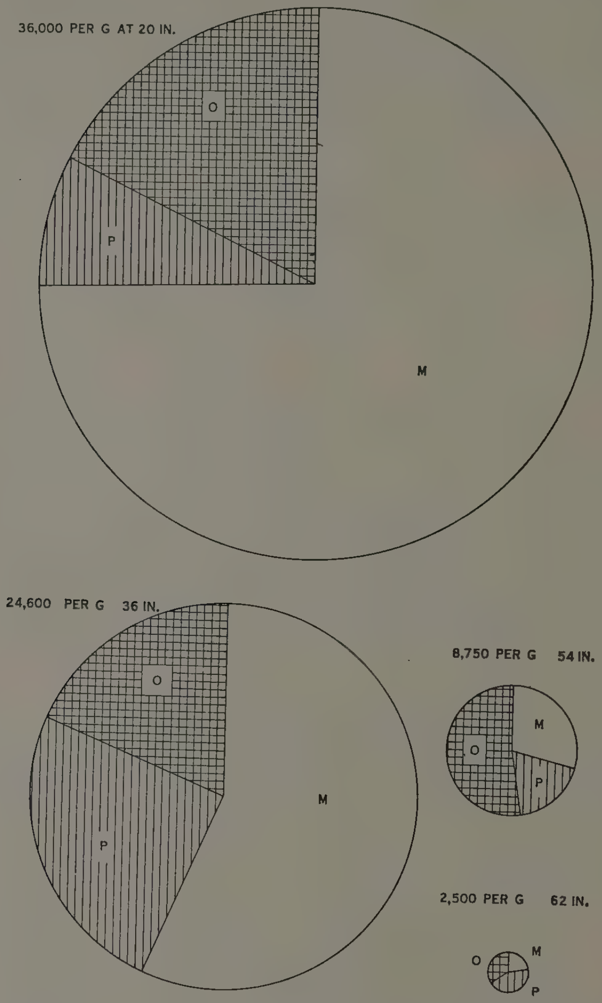


Fig. 3.—Four charts illustrating the size of the fungal population at various levels of the ortstein. At 54 in. the pipe was fading out, at 62 in. the chart represents the C horizon. *M* = *Mortierella ramanniana; P* = *Penicillium* spp.; *O* = other fungi.

An analysis of the fungal population of the B horizon showed no marked change with increasing depth, *Mortierella ramanniana* is the dominant member. Figure 3 shows the relative sizes of the fungal population at various levels of the coffee-rock. The proportion of *M. ramanniana* and *Penicillium* spp. to other forms is indicated by the shading within the circles. *Penicillium adametzi* and *P. nigricans* extend right through the samplings and they are the dominant species of this genus.

VI. The Litter Fungi

The amount of litter found on the soil surface is very sparse and in many places the soil is bare. Samples of the plant remains lying under the various low shrubs which characterize the heath flora were scraped carefully into sterile containers. In the laboratory the leaves etc. were ground between sterile slides, the powdered litter was then put into petri dishes, and some of these poured with malt agar at 45°C. Others were placed in a steam sterilizer and held at 98°C for 3-6 min; after steaming all the plates were poured with malt agar and incubated at 25°C.

In addition fallen leaves from individual species were collected separately and were placed in sterile dishes which were poured with malt agar at 45°C. The fungi developing from such leaves were similar in type to those coming from the pounded material, with the exception of a form of special interest which developed from the leaves of *Monotoca scoparia* R. Br. It was determined as *Verticicladium trifidum* Preuss. This fungus is known to occur on rotting or fallen needles of *Pinus sylvestris* L. in Europe (Hughes 1951). Its occurrence on *Monotoca* leaves extends its geographical range to Australia and its presence on sclerophyllous dicotyledonous leaves suggests that it may be a cosmopolitan litter form. Further work is in progress in this connection.

The appearance of *Pullularia pullulans* in both series of plates emphasizes its widespread distribution in the litter. Smit and Wieringa (1953) have shown that when yellowed leaves of a variety of plants just at the point of abscission or when they have just fallen were shaken up in sterile water, then loops plated out on agar, the resulting flora consisted almost exclusively of *P. pullulans*. They consider that this species is the chief pectin-splitting organism in the early decomposition of litter. *P. pullulans* is a cosmopolitan organism to be found according to our experience on most living plant parts in Victoria and its occurrence on the sparse litter covering the Frankston soil is indicated by its regular appearance on the plates.

A comparison of the flora on the steamed litter plates with that on the unsteamed dishes shows that the Phycomycetes are suppressed by this heat treatment, as well as many fungi that are reproduced by phialospores and are not naturally heat-resistant. *Penicillium pusillum* and *P. rolfsii,* two sclerote-forming species, were isolated only from the unsteamed

TABLE 11

EFFECT OF STEAMING ON THE ISOLATION OF FUNGI FROM THE DEBRIS LYING ON SOIL

Fungus	Unsteamed	Steamed 3-6 Min
Absidia glauca	+	−
Cladochytrium replicatum	+	−
Fusarium sp.	+	−
Gliomastix convoluta	+	−
*Mortierella vinacea**	+	−
M. ramanniana	+	−
Mucor fragilis	+	−
M. mucedo	+	−
Penicillium adametzi	+	−
P. canescens	+	−
P. frequentans	+	−
P. nigricans	+	−
P. ochro-chloron	+	−
P. paxilli	+	−
P. pusillum	+	−
P. rolfsii	+	−
P. spinulosum	+	−
P. urticae	+	−
P. waksmani	+	−
P. vermiculatum	+	−
Trichoderma viride	+	−
Amphichaete grevilleae	+	+
Penicillium claviforme	+	+
P. thomii	+	+
P. verruculosum	+	+
Pullularia pullulans	+	+
Sordaria fimicola	+	+
Alternaria fasciculata	−	+
Aspergillus caespitosus	−	+
A. fischeri	−	+
A. fumigatus	−	+
Humicola grisea	−	+
Neurospora tetrasperma	−	+
Nigrospora sphaerica	−	+
Penicillium fuscum	−	+
P. granulatum	−	+
P. lapidosum	−	+
P. rugulosum	−	+
Pestalotia sp.		
Sepedonium chrysospermum	−	+
Sordaria sp.	−	+
Spegazzinia sp. nov.	−	+

* Linnemann (1941).

samples. No physiological studies have been reported on these fungi although they are recognized as characteristically present on organic material undergoing slow aerobic decomposition. They do not appear to be favoured by subjection to steaming. *Penicillium vermiculatum* also occurred only on plates from unsteamed material although this form has been recorded as resistant to steaming (Warcup 1951*b*).

The fungi appearing on *both* samples or *only* on the *steamed* litter can be separated into two groups:

(*a*) *Ascosporic and Sclerotial Forms*

Sordaria fimicola appeared commonly on both untreated and treated plates. This species is coprophilous in habit so that softening of the spore wall occurs in the alimentary tract; unsteamed litter samples were rich in this form and certain of the spores resisted the heat treatment.

Aspergillus fischeri is an ascosporic mould, world-wide in distribution with a high temperature optimum for growth (37°C or higher), it is closely allied taxonomically with *A. fumigatus,* also characteristic of the heat-treated litter. This is another cosmopolitan mould and is said to occur with particular frequency on vegetable matter undergoing slow decomposition (Thom and Raper 1945). It grows well at 45-50°C and so is able to operate within a range where most fungi are excluded and its activities would be well suited by the high summer temperatures to which the exposed and sparse litter is subject.

Aspergillus caespitosus does not form perithecia or typical sclerotes but its growth is characterized by the presence of numerous thick-walled hülle cells and so this form would have a certain heat resistance. It has been recorded from the dry warm soils of Texas, Arizona, and adjoining areas.

The heat activation of the ascospores of *Neurospora tetrasperma* was responsible for the appearance of this mould from the steamed samples, for it is well known that without such heat activation the percentage germination of *Neurospora* ascospores is almost insignificant.

Penicillium lapidosum possesses sclerotia which are unusually heat-tolerant. It is reported in the literature (Williams, Cameron, and Williams 1941) that this mould was isolated in America from soil samples associated with blueberry bushes which had been heated in the laboratory to 180°F. for 25 min. *P. thomii* is ubiquitous and cosmopolitan in surface soil and litter and has been reported to be especially active in the decomposition of tannin. Sclerotial formation enables this fungus to withstand the heat treatment.

(*b*) *Fungi Forming Neither Ascospores nor Sclerotia*

Two types of fungi are recognized in this grouping.

(i) *Fungi Reproducing by Phialospores.*—This group is represented by five species of *Penicillium*—*P. claviforme* and *P. verruculosum,* which appeared on both series of plates, and *P. fuscum, P. granulatum,* and *P. rugulosum* only on the steamed litter.

(ii) *Fungi Forming Some Type of Thick-walled Spore* (*thallospores*).—The thick resistant spore wall enables these fungi to withstand the heat treatment. This group was not isolated from the untreated litter; probably they were suppressed by the fast-growing fungi, e.g. Mucorales and *Trichoderma. Humicola grisea* was the commonly isolated fungus of this group, all the plates yielding one or two colonies. A new species of *Spegazzinia* was noteworthy, for this is an uncommon genus and, unlike the other fungi recorded, is not generally listed as a member of the soil flora.

Many of the fungi then, which bring about slow decomposition of the litter in this heath community, could survive the long, hot, dry summer periods because of the presence of a resistant stage in their life cycle.

VII. EFFECT OF STEAMING ON THE SOIL FUNGI

Warcup (1951*b*) discussed the effect of partial steaming on fungus colonization of soil (Kettering loam). He found that steaming soil for 4 min had a twofold effect, in that the normal soil species were reduced in number or suppressed, and many forms unrecorded by him from untreated soil appeared abundantly, including six ascosporic fungi. In the untreated samples he noted only one such ascosporic type. He considered that they were crowded out of the unsteamed soil plates by fast-growing fungi, chiefly Mucorales.

Samples of the Frankston soil were heated for 4 min, using the method outlined by Warcup. Samples (125 g) were taken from the A_1 horizon at 1-2½ in. (care was taken to exclude any traces of litter); others from the A_2 horizon at 24-26 in., and others from the B level (ortstein or coffee-rock at 38-40 in.).

The fungi included in Table 12 were isolated by the use of Warcup's soil plate technique. It includes no form not already listed by the dilution plate method. The outstanding feature is the practically complete suppression of all forms after the brief steaming period. No ascosporic or sclerotial forms appeared. Care was taken in preparing the samples to avoid the surface soil so that litter remnants would be excluded. Sclerotial forms, e.g. *Penicillium lapidosum* and *P. thomii,* have been isolated previously by us during our study of the Frankston soil, and Thrower (1954) also recorded both these species from the free soil and from the rhizosphere of some of the heath plants. His results are represented in Table 13.

These results represent an equal number of isolation experiments for both soil and rhizospheres. No active precautions were taken in his isolations to exclude litter or dead and decaying plant parts around the crowns of the growing plants. The great increase of *P. lapidosum* and *P. thomii* in the rhizosphere in all cases presents a very striking distribution for these fungi, the significance of which is not clear but supports

TABLE 12

EFFECT OF STEAMING ON THE FUNGAL POPULATION OF SAMPLES OF SOIL TAKEN FROM VARYING DEPTHS IN THE SOIL PROFILE

Fungus	Horizon:	A_1		A_2		B	
	Depth (in.):	1-2½		24-26		38-40	
	Steaming Time (min):	0	4	0	4	0	4
Absidia glauca		+	—	+	—	—	—
Aspergillus fumigatus		+	—	—		—	—
A. sydowi		+	—		—	—	—
A. sp. nov. (1)		+	—	—	—	—	—
A. sp. nov. (2)		+	—	+		—	—
Cladosporium herbarum		+	+	—	—	—	—
Fusarium sp.		+	—				—
Gliomastix convoluta		+	—	—		—	—
Mortierella ramanniana		+	—	+	—	+	—
M. vinacea		+	—	+	—	+	—
M. stylospora		+	—	—	—	—	—
Papularia sphaerosperma		+	—	—	—	—	—
Penicillium adametzi		+	—	+		—	—
P. brevicompactum		+	+	—	—	—	—
P. canescens		+	—	—	—	—	—
P. cyaneo-fulvum		+	—	—	—	—	—
P. cyaneum		—	—	—	—	—	+
P. frequentans		—	+	—	—	—	—
P. funiculosum		+	—	+	—	—	—
P. fuscum		+	—	—	—	—	—
P. godlewskii		+	—	—	—	—	—
P. javanicum		+	—	—	—	—	—
P. meleagrinum		+	—	+	—	+	—
P. nigricans		+	—	+	—	+	—
P. verruculosum		+	—	—	—	—	—
P. waksmani		+	+	—	—	—	—
P. sp. nov.		+	—	—	—	—	—
Pythium sp.		+	—	+	—	+	—
Rhizopus nigricans		+	—	—	—	—	—
Scopulariopsis brevicaulis var. *A.*		+	—	—	—	—	—
S. brevicaulis var. *B*		+	—	—	—	—	—
Trichoderma viride		+	+	—	—	—	—

the suggestion that sclerotial and possibly ascosporic types characterize the fungal flora of plant debris and are not typical members of the free soil population.

VIII. Discussion

When a quantitative estimate of the activity of fungi in soil is made by the use of the dilution plate method and a high "count" results it is often said that the result reflects a high sporing capacity of a few fungi rather than a high level of fungal activity in the soil. In discussing the significance of such plate counts Garrett (1952) suggested that if this interpretation is correct the validity even of the general conclusion that fungi are more active in acid than in neutral or alkaline soils may be queried.

Table 13

NUMBER OF TIMES SOME SCLEROTIAL PENICILLIA WERE ISOLATED FROM FREE FRANKSTON SOIL AND FROM THE RHIZOSPHERES OF PLANTS GROWING IN IT

Fungus	Soil	Rhizospheres of				
		Epacris	*Lepidosperma*	*Leucopogon*	*Hibbertia*	*Dillwynia*
Penicillium lapidosum	2	32	14	29	13	29
P. thomii	5	30	10	10	8	1
Other sclerotial penicillia	—	5	1	2	3	1
Total	7	67	25	41	24	31

Early in our study of the sandy podzol soil it was thought that a comparison of the results obtained by the dilution method with the results from the direct observational method would yield data which might help to interpret the relationship of developing colonies on plates to mycelia of spore origin. When the two techniques were compared it became clear that high counts are not to be related to sporing capacity but they indicate a measure of mycelial activity. This result was confirmed by Skinner, Jones, and Mollison (1952).

Direct examination of soil will occasionally reveal spores, but in our experience they are not at all numerous. A recent article by Dobbs and Hinson (1953) deals with the inhibition of germination of spores in moist soil. Using a strain of *Penicillium frequentans* they found that spore germination was completely inhibited in 18 different types of soil. Incomplete inhibition, amounting to a minute fractional percentage of spores compared to controls was found in three subsoils. The inhibition was not shown by old dried samples of soil and these when moistened became mouldy, as with autoclaved soils. The fungi used in their tests have been in the main isolated from the soils tested. Hessayon (1953) observed that *Trichothecium roseum* spores failed to germinate in any of the unsterilized soils he used in his experiments, even when the humidity and temperature were varied, although growth of a mycelial inoculum took place. Dobbs and Hinson stated, "that spores must lie dormant in soil is an inescapable deduction from the fact that they germinate in large numbers whenever soil is placed in contact with nutrient media". This conclusion is based on the accepted idea that soil dilution plates favour the heavily sporing sugar fungi, a point which is contested in this paper. However, the inhibition of spore germination by soil emphasizes the suggestion that it is the mycelial state that is predominant in the soil population, a point borne out by the fact that mycelia growing over Rossi-Cholodny slides are most often sterile.

Other techniques have been designed more recently in an attempt to add to our knowledge of the life of fungi in the soil. Of these Chesters' method has been discussed earlier. By its use the quick-growing spreading forms close to the capillaries reach the agar in the tubes and a list of fungi from any soil compiled by the use of this method is necessarily very incomplete, for the design of the tubes and the use of agar make it both restrictive in a mechanical way and selective, for it depends again on the use of some form of nutrient agar. Any list of fungi obtained from soil by this method does not give an adequate expression of the fungal population and no claim to dominance of any form should be made from such results. Garrett (1952) made a comparison between Chesters' list of dominant genera, obtained from cultivated and pasture soils, with one compiled by Waksman, who used the dilution plate method. Garrett considered that Waksman's list "reflects the artificial preponderance of heavily sporing fungi characteristic of the dilution plate method".

That this is not so is proved by the results obtained from soil when the dilution plate method is directly compared with the direct observational method of Jones and Mollison. The free soil fungal population is a characteristic one, and *Penicillium, Mortierella, Mucor, Aspergillus, Trichoderma,* etc. are dominant genera in this complex. A list made from the plate method is not an artificial one and soil mycologists must come to accept such genera as *Mortierella, Penicillium,* and *Aspergillus* as dominant and active members of the soil population, not as an artificial expression produced by the use of a particular method.

Warcup's (1950) soil plate method and Waksman's (1916) method depend upon the use of the grosser soil inocula on the agar plates. According to Garrett this "minimizes the advantage of heavily sporing fungi". This method was tried in the course of this work but the plates quickly became overrun with the numerous fungal colonies and no advantage was gained by its use. It has been claimed that a greater range of species may be isolated as compared with that obtained by the use of other methods. Warcup gave a list of 110 species isolated by him from five soils. The list of species from the Victorian podzol obtained by the dilution plate method includes 103 species, a very wide range from one soil type. Warcup's method of recording the numerical frequency of species, not as numbers of colonies per plate but simply as present or absent on the individual isolation plate, gives an unbalanced picture of the population as the number of colonies of each species on a plate does indicate the relative dominance of any particular species.

The fungal flora of the soil can be said to be cosmopolitan in general type although a few species may be more or less restricted to a particular kind of soil. The genus *Zygorrhynchus* offers an exception to this generalization, for although according to Waksman (1927) this genus has the widest geographical distribution of all soil fungi, it has only been isolated once from an Australian soil (Jensen 1934) and has never been isolated from the sandy podzol under discussion, although Warcup (1951*a*) recorded *Zygorrhynchus vuillemini* Namysl. as even more common in his two acid soils than *Mortierella ramanniana.* One species of *Mortierella, M. stylospora,* present in the podzol, has only been recorded from Australian soils (Dixon-Stewart 1932). We have also isolated three undescribed species of *Aspergillus,** an undescribed species of *Penicillium,* and an undescribed species of a rare genus, *Spegazzinia. Aspergillus* sp. nov. 1 is a common fungus in the podzolic soil and is perhaps characteristic of it as it has not been isolated from other soil types.

Among the fungi recovered from litter or dung lying on the soil, some were, so far as our observations go, confined to this habitat. All such forms were characterized by the possession of a resistant stage in their life cycle, e.g. *Aspergillus fischeri, Neurospora tetrasperma, Nigrospora sphaerica, Penicillium rolfsii,* and *P. vermiculatum.* These represent the fungal organisms responsible for much of the decay of the plant remains on the soil surface. Of the other litter fungi which were also found in soil, some appear to be associated in the soil itself, more particularly with decaying plant parts, e.g. *Penicillium claviforme, P. gladioli, P. lapidosum, P. pusillum,* and represent an extension into the soil of litter forms. The remaining isolates were also represented throughout the general soil population.

The great dominance of *Mortierella ramanniana* over all the other fungi in the A and B horizons seems characteristic of this acid soil, which nevertheless has a varied fungal flora. This is in contrast to Warcup's acid soil *E* where relatively few species were present and these were mainly *Penicillium* spp.

IX. ACKNOWLEDGMENTS

We are indebted to some of the students in the senior ecology class, Botany Department, University of Melbourne, for the soil analysis and the photographs used in Plates 1 and 2.

---

* These fungi will be described in a separate contribution.

X. References

Bisby, G. R., Timonin, M. I., and James, N. (1953).—Fungi isolated from soil profiles in Manitoba. *Canad. J. Res.* C **13**: 47-65.

Brierley, W. B., Jewson, S. T., and Brierley, M. (1927).—The quantitative study of soil fungi. *Proc. 1st Int. Cong. Soil Sci.* **3**: 48-71.

Brown, P. E., and Benton, T. H. (1930).—Microbiological studies of some typical Iowa soil profiles. Iowa Agric. Exp. Sta. Res. Bull. No. 132.

Burges, A. (1939).—Soil fungi and root-infection — A review. *Broteria* 8: 64-81.

Burges, A. (1950).—The downward movement of fungal spores in sandy soil. *Trans. Brit. Mycol. Soc.* **33**: 142-7.

Chesters, C. G. (1940).—A method of isolating soil fungi. *Trans. Brit. Mycol. Soc.* **24**: 352-5.

Chesters, C. G. (1948).—A contribution to the study of fungi in the soil. *Trans. Brit. Mycol. Soc.* **30**: 100-17.

Cookson, Isabel (1937).—On *Saprolegnia terrestris* sp. nov., with some preliminary observations on Victorian soil Saprolegniales. *Proc. Roy. Soc. Vict.* **49**: 235-43.

Dixon, Dorothy (1928).—The microorganisms of cultivated and bush soils in Victoria. *Aust. J. Exp. Biol. Med. Sci.* **5**: 223-32.

Dixon, Dorothy (1930).—The microorganisms of the Tertiary red sands near Melbourne, Victoria. *Aust. J. Exp. Biol. Med. Sci.* **7**: 161-9.

Dixon-Stewart, Dorothy (1932).—Species of *Mortierella* isolated from soil. *Trans. Brit. Mycol. Soc.* **17**: 208-20.

Dobbs, C. G., and Hinson, W. H. (1953).—A widespread fungistasis in soils. *Nature* **172**: 197-9.

Garrett, S. D. (1952).—The soil fungi as a microcosm for ecologists. *Sci. Progr.* **40**: 436-50.

Gilman, J. C. (1945).—"A Manual of Soil Fungi." (The Collegiate Press Inc.: Iowa.)

Gilman, J. C., and Abbott, E. V. (1927).—A summary of the soil fungi. *Iowa St. Coll. J. Sci.* **1**: 225-345.

Gray, P. H. H., and McMaster, N. B. (1933).—A microbiological study of podsol soil profiles. *Canad. J. Res.* C **8**: 375-89.

Gray, P. H. H., and Taylor, C. B. (1935).—A microbiological study of podsol soil profiles. II. Laurentian soils. *Canad. J. Res.* C **13**: 251-5.

Hessayon, D. G. (1953).—Fungitoxins in the soil. II. Tricothecin, its production and inactivation in unsterilized soils. *Soil Sci.* **75**: 395-404.

Hughes, S. J. (1951).—Studies on micro-fungi. IX. *Calcarisporium*, *Verticicladium* and *Hansfordia* (gen. nov.) *C.M.I. Mycol. Pap.* **43**: 1-25.

James, N., and Sutherland, Marjorie L. (1939*a*).—The accuracy of the plating method for estimating the numbers of soil bacteria, *Actinomyces*, and fungi in the dilution plated. *Canad. J. Res.* C **17**: 72-86.

James, N., and Sutherland, Marjorie L. (1939*b*).—The accuracy of the plating method for estimating the numbers of bacteria and fungi from one dilution and from one aliquot of a laboratory sample of soil. *Canad. J. Res.* C **17**: 97-108.

Jensen, H. L. (1934).—Contributions to the microbiology of Australian soils. 1. Numbers of micro-organisms in soil, and their relation to certain external factors. *Proc. Linn. Soc. N.S.W.* **59**: 101-17.

Jones, P. C. T., and Mollison, J. E. (1948).—A technique for the quantitative estimation of soil micro-organisms. *J. Gen. Microbiol.* **2**: 54-69.

Leeper, G. W. (1948).—"Introduction to Soil Science." (Melb. Univ. Press.)

Linnemann, Germaine (1941).—Die Mucorineen — Gattung *Mortierella* Coemans. (Gustav Fischer: Jena.)

McLENNAN, ETHEL I. (1928).—The growth of fungi in the soil. *Ann. Appl. Biol.* **15**: 95-109.

McLENNAN, ETHEL I., and DUCKER, SOPHIE C. (1952).—The description and distribution of the species of *Penicillium* Link in some Victorian soils. *Proc. Roy. Soc. Vict.* **64**: 10-71.

MARTIN, T. L., and ANDERSON, D. A. (1943).—Organic matter decomposition, mould flora, and soil aggregation relationships. *Proc. Soil. Sci. Soc. Amer.* **7**: 215-17.

MUNSELL COLOUR COMPANY INC. (1948).—"Munsell Soil Color Charts." (Baltimore.)

SKINNER, F. A., JONES, P. C. T., and MOLLISON, J. E. (1952).—A comparison of a direct and a plate-counting technique for the quantitative estimation of soil micro-organisms. *J. Gen. Microbiol.* **6**: 261-71.

SMIT, J., and WIERINGA, K. T. (1953).—Microbiological decomposition of litter. *Nature* **171**: 794-5.

TIMONIN, M. I. (1938).—The micro-organisms in profiles of certain virgin soils in Manitoba. *Canad. J. Res.* C **13**: 32-46.

THOM, C., and RAPER, K. B. (1945).—"A Manual of the *Aspergilli.*" (Williams and Wilkins Co.: Baltimore.)

THOM, C., and RAPER, K. B. (1949).—"A Manual of the *Penicillia.*" (Williams and Wilkins Co.: Baltimore.)

THROWER, L. B. (1954).—The rhizosphere effect shown by some Victorian heathland plants. *Aust. J. Bot.* **2**: 246-67.

WAKSMAN, S. A. (1916).—Do fungi live and produce mycelium in the soil? *Science* **44**: 320.

WAKSMAN, S. A. (1922).—The growth of fungi in the soil. *Soil Sci.* **14**: 153-7.

WAKSMAN, S. A. (1927).—"Principles of Soil Microbiology." (Williams and Wilkins Co.: Baltimore.)

WARCUP, J. H. (1950).—The soil-plate method for isolation of fungi from soil. *Nature* **166**: 117-18.

WARCUP, J. H. (1951*a*).—The ecology of soil fungi. *Trans. Brit. Mycol. Soc.* **34**: 376-99.

WARCUP, J. H. (1951*b*).—Soil steaming: a selective method for the isolation of Ascomycetes from soil. *Trans. Brit. Mycol. Soc.* **34**: 515-18.

WHINCUP, SYLVIA (1944).—Superficial sand deposits between Brighton and Frankston, Victoria. *Proc. Roy. Soc. Vict.* **56** (1): 53-76.

WILLIAMS, C. C., CAMERON, E. J., and WILLIAMS, P. B. (1941).—A facultatively anaerobic mould of unusual heat resistance. *Food Res.* **5**: 69-73.

APPENDIX I

Species	Horizons				
	Litter	Dung	A	B	C
Absidia cylindrospora Hag.			+	+	
A. glauca Hag.	+		+		
Acrostalagmus cinnabarinus Cda.			+		
Acrothecium robustum Gilman & Abbott			+		
Alternaria fasciculata Cooke & Ellis	+		+	+	
Amphichaete grevilleae Loos	+				
Aspergillus caespitosus Raper & Thom		+			
A. fischeri Wehmer	+				
A. flavus Link			+		
A. fumigatus Fres.		+	+		
A. niger van Tieg.			+		
A. repens (Cda.) de Bary			+		
A. sydowi (Bain. & Sart.) Thom & Church			+		
A. terreus Thom			+	+	
A. versicolor Vuill.		+			
A. sp. nov. (1)			+	+	
A. sp. nov. (2)		+	+		
Camarosporium abietis Wilson				+	
Chaetomium globosum Kunze			+		
Cladochytrium replicatum Karling		+			
Cladosporium herbarum Link			+	+	+
Cunninghamella verticillata Paine			+		
Dicoccum asperum Cda.			+		
Fusarium spp. (4)			+		
Gliocladium roseum (Link) Bain.			+		
Gliomastix convoluta (Harz) Mason		+	+		
Helminthosporium anomalum Gil. & Abb.			+		
Hormodendrum sp.			+		
Humicola grisea Traaen	+			+	
Mortierella isabellina Oud.					
M. pusilla Oud.			+	+	
M. ramanniana (Möll.) Linnemann	+		+	+	+
M. stylospora Dixon-Stewart			+	+	+
M. vinacea Dixon-Stewart	+		+		+
Mucor fragilis Bain.			+		
M. griseocyaneus Hag.	+				
M. hiemalis Wehm.				+	
M. mucedo (L.) Fres.	+				
Neurospora tetrasperma Shear & Dodge	+		+		
Nigrospora sphaerica (Sacc.) Mason	+				
Pachybasium hamatum (Bon.) Sacc.				+	
Paecilomyces varioti Bain.			+		
Papularia sphaerosperma (Pers.) von Hohn.			+		
Penicillium adametzi Zal.	+		+	+	+
P. baarnense T. Beyma		+			
P. brevicompactum Dierckx			+	+	
P. canescens Sopp	+		+	+	

APPENDIX I (*Continued*)

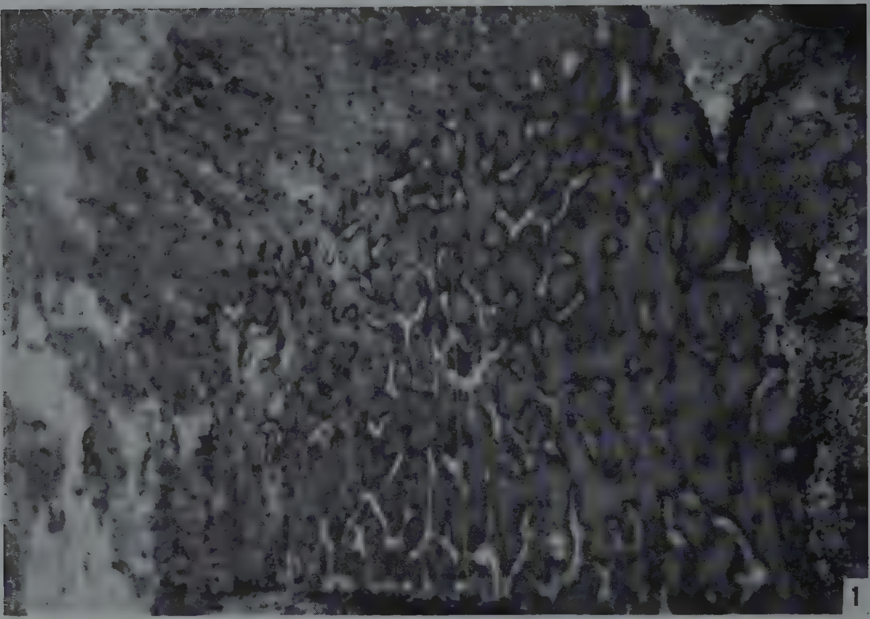
Species	Horizons				
	Litter	Dung	A	B	C
P. chrysogenum Thom				+	+
P. claviforme Bain.	+				
P. cyaneum (Bain. & Sart.) Biourge			+	+	+
P. cyaneo-fulvum Biourge			+		
P. digitatum Sacc.			+	+	
P. diversum Raper & Fennell				+	
P. expansum Link			+	+	+
P. fellutanum Biourge			+	+	+
P. frequentans Westl.	+		+	+	+
P. funiculosum Thom			+	+	+
P. fuscum (Sopp) Raper & Thom	+		+		
P. gladioli Machacek					
P. godlewskii Zal.			+	+	
P. granulatum Bain.	+		+		
P. islandicum Sopp			+		
P. janthinellum Biourge			+	+	+
P. javanicum v. Beyma			+		
P. lapidosum Raper & Fennell	+				
P. martensii Biourge			+		
P. meleagrinum Biourge			+	+	+
P. melinii Thom			+		+
P. nigricans (Bain.) Thom			+	+	+
P. ochro-chloron Biourge		+			
P. paxilli Bain.	+				
P. piscarium Westh.				+	
P. puberulum Bain.					+
P. purpurogenum Stoll			+	+	
P. purpurrescens (Sopp) Raper & Thom			+	+	
P. pusillum Smith	+				
P. raciborskii Zal.				+	
P. restrictum Gil. & Abb.			+	+	+
P. rolfsii Thom	+	+		+	
P. rubrum Stoll					+
P. rugulosum Thom	+		+	+	
P. spinulosum Thom	+		+	+	
P. thomii Maire	+				
P. urticae Bain.	+				
P. vermiculatum Dang.	+		+		
P. verruculosum Peyron.	+		+	+	
P. viridicatum Westl.				+	
P. waksmani Zal.	+		+	+	
P. sp. nov.			+		
Pestalotia caudata Syd.	+				
Phoma humicola Gil. & Abb.			+	+	+
Pullularia pullulans (de Bary) Berkh.	+		+		
Pythium sp.			+	+	
Rhizopus nigricans Ehrenb.			+		+

ECOLOGY OF HEATHLAND SOIL FUNGI

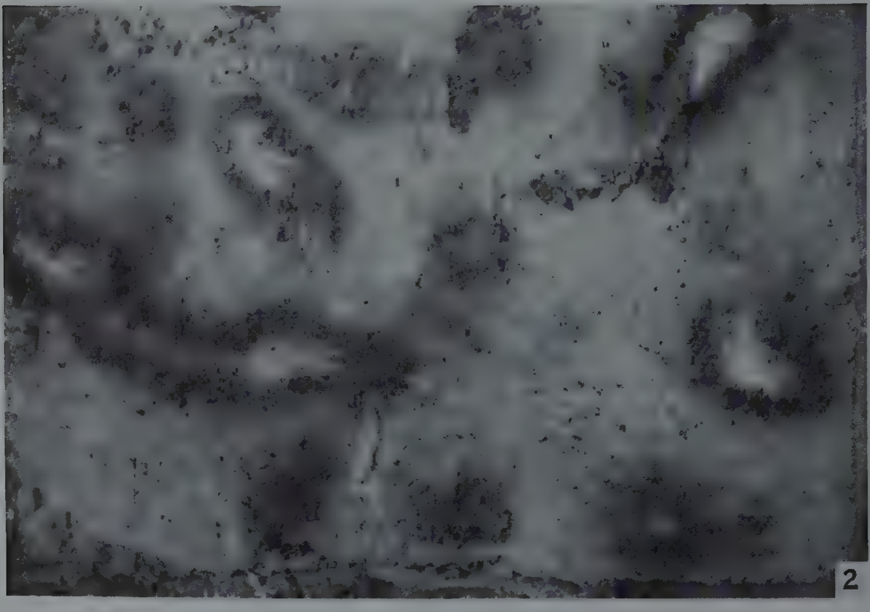
1

2

ECOLOGY OF HEATHLAND SOIL FUNGI

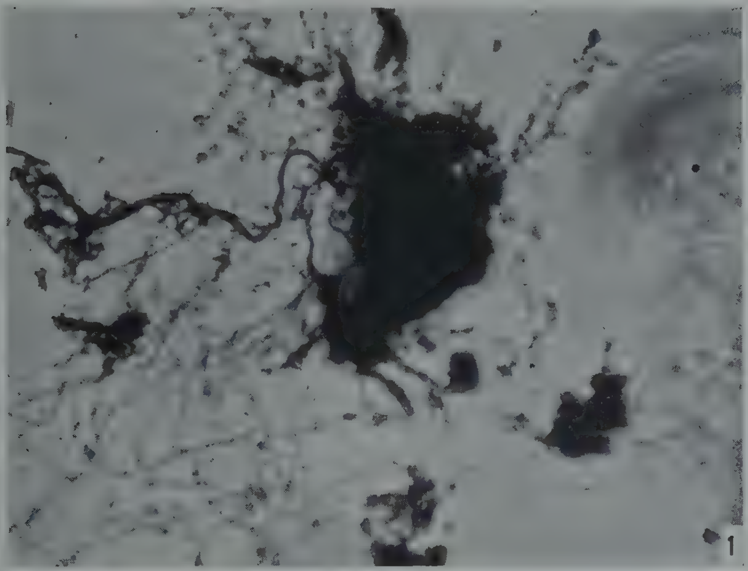


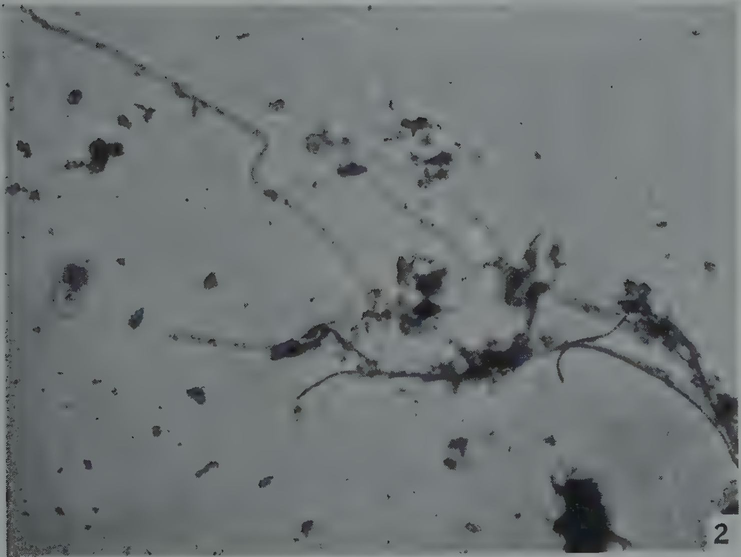
1



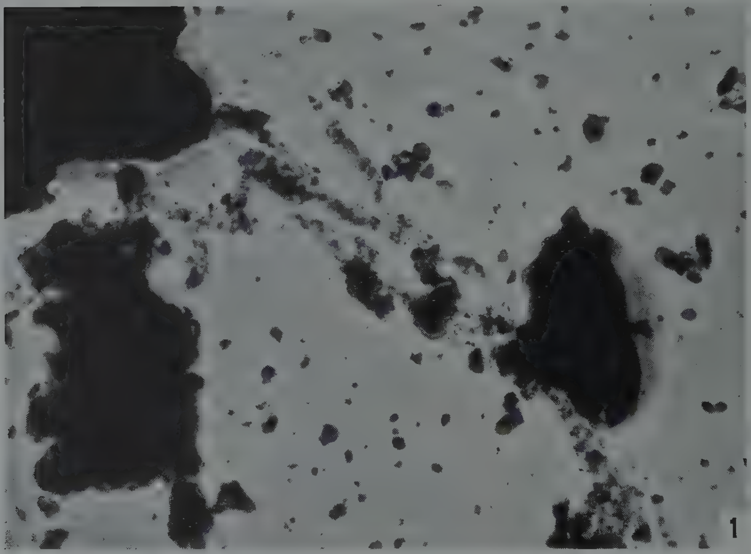
2

ECOLOGY OF HEATHLAND SOIL FUNGI

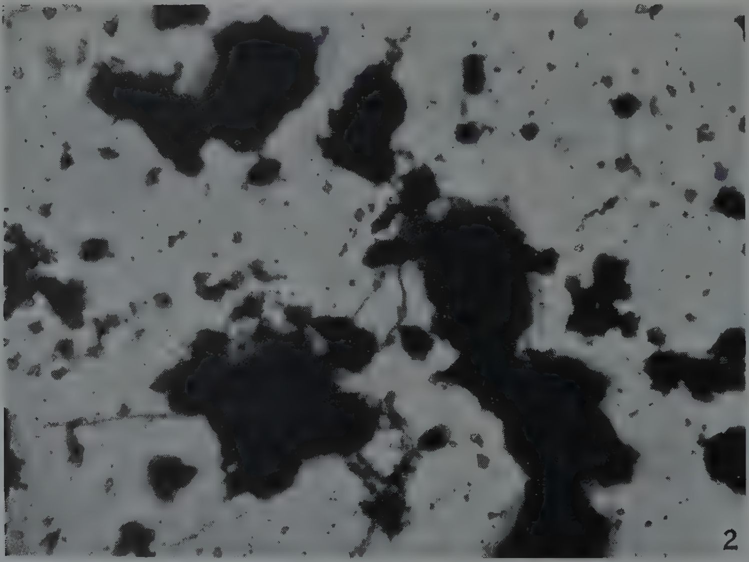

1


2

ECOLOGY OF HEATHLAND SOIL FUNGI



1



2

APPENDIX I (*Continued*)

Species	Horizons				
	Litter	Dung	A	B	C
Scopulariopsis brevicaulis (Sacc.) Bain.					
var. *A*			+		
var. *B*			+		
Sepedonium chrysospermum (Bull.) Fr.	+			+	
Sordaria fimicola (Rob.) Ces. de Not.	+		+		
Spegazzinia sp. nov.	+		+		
Sphaeronaema sp.			+		
Spondycladium xylogenum A. L. Smith			+		
Sporormia intermedia Auersw.			+		
Sporotrichum sp.			+		
Stemphylium botryosum Wallroth			+		
Syncephalis sphaerica van Teigh.			+		
Trichoderma viride Pers.	+		+	+	+
Trichothecium roseum Link	+		+		
Verticicladium trifidum Preuss	+				

EXPLANATION OF PLATES 1-4

PLATE 1

Fig. 1.—Profile of the podzol at Frankston, Vic.

Fig. 2.—Portion of a profile showing (*a*) the leached A_2 horizon, and (*b*) the narrow B horizon (ortstein or "coffee-rock") with the characteristic pipe-like extensions into the C horizon.

PLATE 2

Fig. 1.—Surface view of the soil at the junction of the ortstein and the C horizon after the removal of the A and B horizons. The net-like pattern results from the vertical extensions of the "pipes". The lighter leached areas are surrounded by the dark coffee-rock margins.

Fig. 2.—An enlarged view of portion of a similar surface.

PLATE 3

Portion of slides made by the Jones and Mollison (1948) technique. The soil used came from the A_1 horizon. Note the profuse development of the Phycomycete type of mycelium (*Mortierella ramanniana*).

PLATE 4

Similar slides with soil from the B horizon showing the abundant humus particles, closely enveloped by fungal mycelium.

THE RHIZOSPHERE EFFECT SHOWN BY SOME VICTORIAN HEATHLAND PLANTS

By L. B. THROWER*

(*Manuscript received January* 26, 1954)

Summary

During the period July 1951 to October 1952, a study was made of the fungal population of the soil of a Victorian heathland with reference to the rhizosphere effect exerted by five species of native plants growing there.

Some 45 genera of fungi with 115 species were isolated; of these, 52 species were obtained from the free soil and the rhizosphere, 25 from the soil only, 27 from the rhizosphere, and 11 species were isolated only from dung.

During this period, the numbers of fungal propagules in the free soil, estimated by the dilution-plate technique, varied from 68,500 to 247,600 per gram of oven-dry soil; R/S ratios of 0.6-9.7 were recorded.

A study has been made of the antibiotic and cellulose-decomposing activities, and the nutritional requirements, of the mycoflora. Examination of the soil for N-fixing organisms showed that *Azotobacter* and acid-tolerant aerobes were absent; anaerobes were present in small numbers.

I. INTRODUCTION

The work described was undertaken during the two years 1951-52. It had as its object a study of the soil microorganisms of a heathland at Frankston, Vic., with special reference to the rhizosphere effect exhibited by some of the native plants growing there. It was concerned mainly with the fungal component of the microflora; however, an effort was also made to define the environment, physical and microbiological, in which the roots and fungi existed and exerted their influence.

II. DESCRIPTION OF SOIL AND VEGETATION

The soil investigated was that of the Frankston heath, which is located some 25 miles from Melbourne. According to Whincup (1944) the sandhills in this vicinity, though difficult to classify, are probably barchan dunes. She considered that their formation was due to the action of a north-west wind acting under climatic conditions which were rather drier than those existing at present.

In order to facilitate precise description, mechanical and partial chemical analyses were carried out. The methods employed were those described by Piper (1950) except that soil colour was expressed in terms of the Munsell System (Munsell 1948) following the procedure recommended by Pendleton and Nickerson (1951); the results appear as Table 1. Whereas the physical analysis represents an average value for each

---

* Botany Department, University of Melbourne.

horizon, the soil used for the chemical analysis of the A_1 horizon was taken from samples collected for microbiological examination, so that the values obtained apply to the uppermost 6 in. of soil.

The soil is a sandy podzol consisting of a grey A_1 horizon which merges at about 22 in. into a light grey A_2 horizon. The total depth of the A horizon varies about a mean of approx. 33 in. On top of the mineral soil is a sparse litter of largely undecomposed plant debris.

TABLE 1

RESULTS OF MECHANICAL AND PARTIAL CHEMICAL ANALYSIS OF FRANKSTON SOIL

Character	A_1	A_2	B	C
Depth (in.)	0-22	22-33	33-36	36+
Colour (*a*) Dry	N5.5/- Grey	N8/- White	10 YR 2/2 Very dark brown	10 YR 6/8 Brownish yellow
(*b*) Moist	5 Y 4/1 Dark grey	5 Y 6/1 Grey	10 YR 2/1 Black	10 YR 5/6 Yellowish brown
pH	4.6	4.5	4.8	5.2
Coarse sand (%)	86.1	86.4	86.0	92.6
Fine sand (%)	9.4	9.6	9.2	3.7
Silt (%)	1.6	0.6	1.5	0.5
Clay (%)	2.9	3.4	3.3	3.2
Chloride (water sol.) (%)	<0.01			
Organic carbon (%)	1.5	0.3	1.3	0.25
Nitrogen (%)	0.07			
P_2O_5 (%)	0.007			
Water-holding capacity (%)	28.1	25.8	34.9	25.0

The B horizon is a layer of ortstein some 3-6 in. thick, beneath which is a layer of yellowish sand that constitutes the C horizon. Inspection of the exposed face of a sand-pit showed it to be at least 70 ft deep, and probably it forms a homogeneous layer to the base of the dune.

As the mechanical analysis shows, the coarse sand fraction predominates throughout the profile, remaining fairly constant in the upper three layers and reaching a maximum level in the C horizon.

Content of organic carbon is highest in the A_1, but falls markedly in the A_2 layer; it is high again in the ortstein layer, but lowest in the C horizon. Water-holding capacity follows precisely the same course of variation.

Despite the fact that the heathland is close to the sea, the chloride content of the soil is very low. This would be expected from the low percentage of clay and other colloidal material in a leached soil of this kind.

Apart from scattered clumps of *Eucalyptus viminalis* Labill. in the stunted coastal form, the vegetation consists mainly of xeromorphic shrubs growing to a fairly uniform height of 2-3 ft and beneath which is a ground layer comprising two xeromorphic monocotyledons and some more mesomorphic herbs and mosses. Among the more important species of the shrub layer are *Epacris impressa* Labill., *Leptospermum myrsinoides* Schlech., *Hypolaena fastigiata* R. Br., and *Lepidosperma concavum* R. Br. Seven species of Leguminosae are present, while the ground layer includes four species of Droseraceae. The root systems of the shrubs probably occupy and exploit the soil very thoroughly; often the roots pass into the C horizon. It is known that the vegetation has been burned periodically and fragments of charcoal are embedded fairly deeply in the A horizon. The soil has never been cultivated and during the period 1951-52 no domesticated animals grazed on the heath, although both rabbits and wallabies were present.

Annual rainfall is approximately 28 in., with January and February the only months during which the average is less than 2 in.; these months also have the highest mean maximum temperatures (76.5 and 77.1°F respectively). Data for the period 1931-40 show that there is an influential rain period of 11 months duration, February being the only month during which P/E is less than 0.33. The three summer months have an average ratio of 0.41, but it was found that the soil moisture may be reduced to 2.0 per cent. in late summer.

III. Methods of Isolation

There is now fairly general agreement that the several methods of isolating fungi from the soil provide results that supplement each other. Accordingly, the dilution-plate method was used to get a quantitative estimate of the microflora and other methods were employed to obtain additional qualitative information.

Each month, samples of root-free and rhizosphere soil were examined by the dilution-plate technique. The species of higher plants selected for rhizosphere studies were: *Dillwynia floribunda* Sm. (Leguminosae), *Epacris impressa* Labill. (Epacridaceae), *Hibbertia fasciculata* R. Br. (Dilleniaceae), *Lepidosperma concavum* R. Br. (Cyperaceae), *Leucopogon virgatus* R. Br. (Epacridaceae).

(*a*) *Collection of Soil Samples*

For samples of rhizosphere soil, a block of soil containing the roots of the desired plant with the aerial parts intact was taken. For comparison, blocks of soil were removed to a depth of 6 in. from a patch which was bare of vegetation; this soil had a fairly dense mass of roots ramifying through it. The blocks were wrapped separately in sterile paper for transport to the laboratory.

(*b*) *Dilution Plates*

The method used for preparing the dilution plates was that recommended by James and Sutherland (1939), in which an initial 1: 50 dilution is raised to 1: 5000 in one step; from each original suspension three flasks of 1: 5000 dilution are prepared and one plate is poured from each of the final dilutions.

Soil taken from the bare patches was passed through a sterile 2-mm sieve to remove all roots; these samples were considered as "root-free soil". Three or six 1: 50 dilutions were prepared from these samples, each containing approximately 25 g of soil on a dry-weight basis. Malt extract agar was the medium used for isolation and the plates were incubated at 24°C. Finally, two samples of sieved soil were dried at 105°C so that the original dilutions could be expressed on a dry weight basis.

In sampling the rhizosphere soil, the initial dilutions were made in 1-l. flasks containing 500 ml of sterile water. The roots were gently shaken to remove all surplus soil and were then inserted into the flask, the aerial portion being severed at ground level. After higher dilutions and plates had been prepared as described above, the suspended soil was recovered by removing the roots and passing the contents of the flask through a filter; the roots were washed and the washings also passed through the filter. The roots and filter paper containing the soil were dried separately at 105°C so that the weight of soil originally suspended could be found.

(*c*) *Other Methods of Isolating Fungi*

Soil plates (Warcup 1950) were prepared from fresh soil and from soil that had been steamed for 3 min at 100°C as well as from fresh and steamed rabbit and wallaby dung. The latter substrates were examined as possible sources of some Ascomycetes that had been isolated from the soil. Some hemp-seed baits were used to isolate lower Phycomycetes.

(*d*) *Cellulose-decomposing Organisms*

Attempts were made to isolate microorganisms capable of decomposing cellulose by using deep and shallow tubes of liquid medium containing strips of filter paper (Fred and Waksman 1928, pp. 133-4) and selective plating methods as described by Cunningham (1947).

(*e*) *Nitrogen-fixing Organisms*

Soil from the A_1 horizon was examined qualitatively for organisms capable of fixing atmospheric nitrogen. Flasks of mannite medium (Curie 1931) were inoculated with soil and examined for the formation of a pellicle and the presence of cells resembling those of *Azotobacter*. For *Clostridium,* deep tubes of melted glucose agar (Fred and Waksman 1928, p. 11) were inoculated with soil, kept at 80°C for 10 min, and, after rapid cooling, were incubated at 30°C. Samples of soil were sent to Dr. Y. T. Tchan, Macleay Bacteriologist at the Linnean Society of N.S.W., who kindly examined them for aerobic, acid-tolerant, nitrogen-fixing bacteria (Tchan 1952).

IV. General Description of the Soil Microflora

Some of the fungal colonies could be recognized from habit alone so that finally the standard procedure with the dilution plates was to isolate only a representative sample of the population from the plate; such isolates were transferred to slopes of malt extract agar. At the same time the number of occurrences of each species or isolation-type was recorded. In the selective methods only those colonies that appeared to be of special interest were taken.

During the period of study more than 3000 isolations were made from dilution plates, while some 300 colonies were obtained by selective methods.

A list of the fungi and Actinomycetes isolated is given in Table 2, which also records the habitats from which they were obtained. A few species which were isolated only from rabbit or wallaby dung are recorded also since they would eventually pass into the soil.

In all 45 genera of fungi with 115 species were isolated. Two distinct types remained sterile in culture and these have been classified as "Dark and Pale hyphal forms"; the former was much more abundant and it is interesting to note that Warcup (1951) also encountered numerous "non-sporing, dark-coloured Hyphomycetes".

Of the genera isolated, *Penicillium* had by far the greatest number of species (35), but only one of these produced asci, and that species was isolated from dung. *Aspergillus* was represented by eight species, and one of the ascosporic forms was isolated from dung. *Fusarium* and *Mucor* were represented by seven and five species respectively and *Absidia* by five. Pythiaceous fungi were very common but repeated attempts to induce them to produce the sexual stage were unavailing and most of them have been grouped into two form-species.

Basidiomycetes were quite abundant on the heath during the autumn and winter. In addition, microscopic examination of some plants revealed hyphae with clamp connections twining around the roots. No basidiomycetes were isolated despite this evidence of their presence in the free soil and rhizosphere.

Rhodotorula and other yeasts occurred occasionally on the plates; they seemed to be relatively more abundant when the soil was fairly dry. Bacteria rarely occurred on the dilution plates, but were sometimes found on the soil plates. It would appear that bacteria are relatively not abundant in the Frankston soil, probably because of the strongly acid reaction and, in addition, their development in culture was inhibited by

TABLE 2

LIST OF SPECIES ISOLATED FROM SOIL AND RHIZOSPHERE

Species	Source of Isolation						
	Soil	*Epac.*	*Leuc.*	*Lep.*	*Hib.*	*Dil.*	Other*
Phycomycetes							
Oomycetes							
Pythium papillatum (?) Matthews	+						
P. sp. *A*	+	+	+	+	+	+	
P. sp. *B*	+	+	+	+	+		
Zygomycetes							
Absidia butleri Lend.						+	
A. cylindrospora Hagem	+	+	+	+	+	+	*H.s.*
A. glauca Hagem	+					+	
A. orchidis (Vuill.) Hagem		+	+	+			
A. spinosa Lend.					+		
Circinella tenella (?) van Tieg.	+						
Cunninghamella verticillata Paine	+	+	+			+	Rab. S. C.
Mucor attenuatus Linn.							Rab.
M. genevensis Lend.							Wal.
M. hiemalis Wehm.	+			+		+	*H.s.*
M. jansseni Lend.	+						
M. spinosus van Tieg.						+	
Rhizopus arrhizus Fisch.							Wal.
R. nigricans Ehren.	+		+				
Mortierella isabellina Oud.	+	+	+	+		+	*H.f.*; *L.m.*
M. ramanniana Möll.	+	+	+	+	+	+	*H.f.*; *L.m.*
M. pusilla Oud.	+	+	+	+		+	
M. vinacea Dixon-Stewart	+					+	
M. stylospora Dixon-Stewart	+	+	+	+	+	+	
Ascomycetes							
Plectomycetes							
Aspergillus fischeri Wehm.							Rab.
A. nidulans (Eidam.) Wint.							S.s.
Byssochlamys fulva Olliver & Smith							S.s.
Penicillium baarnense van Beyma							Wal.
Thielavia sp. (?)	+						
Pyrenomycetes							
Ceratostoma Sacc. sp. (?)	+						Wal.
Chaetomium globosum Kunze	+						C±
Neurospora tetrasperma Shear & Dodge	+			+			
Pleospora sp.	+						
Sordaria fimicola (Rob.) Ces. de Not.	+						Rab.
Sporormia intermedia (?) Auers.	+						
Fungi Imperfecti							
Moniliales							
Moniliaceae							
(Gloiosporae)							
Gliocladium roseum (Link) Bain.	+		+	+			
Oospora roseo-flava Sacc.			+				
O. variabilis (Lind.) Lindau	+		+	+	+	+	*H.f.*
Trichoderma viride Pers. ex. Fr.	+	+	+	+	+	+	*H.f.* C±
(Xerosporae)							
Aspergillus flavus Link	+		+				

TABLE 2 (*Continued*)

Species	Source of Isolation						
	Soil	*Epac.*	*Leuc.*	*Lep.*	*Hib.*	*Dil.*	Other*
A. fumigatus Fres.	+	+	+	+	+	+	S.s. C
A. niger van Tieg.							Wal.
A. versicolor (Vuill.) Tirab.	+						
†*A.* sp. 6	+	+	+	+	+	+	*H.f.; H.s.*
†*A.* sp. 7							
A. sp. 2603/27		+			+		Rab.
A. sp. 1107/4	+						
Botrytis cinerea Pers.	+			+			
Botrytis sp. (?)	+						
Helicoon fuscosporum Lind.							Rab.
Paecilomyces varioti Bain.	+						
Penicillium adametzi Zal.	+	+	+	+	+	+	
P. brevicompactum Dierckx	+	+	+	+	+	+	
P. canescens Sopp	+	+	+	+	+	+	
P. chrysogenum Thom				+		+	
P. claviforme Bain.	+	+	+		+		
P. cyaneum (Bain. & Sart.) Biourge		+		+			C
P. digitatum Sacc.	+						
P. expansum Link	+	+	+	+	+	+	
P. fellutanum Biourge	+	+		+		+	
P. frequentans Westl.	+	+	+	+	+	+	*H.f.*
P. funiculosum Thom	+	+					
P. gladioli Mach.		+					
P. godlewskii Zal.	+	+	+	+	+	+	
P. islandicum Sopp	+	+		+	+	+	
P. janthinellum Biourge	+	+	+	+	+	+	
P. lapidosum Raper & Fennell	+	+	+	+	+	+	*H.f.;* Wal. *H.s.;* Rab.
P. martensii Biourge	+		+				
P. meleagrinum Biourge						+	
P. melinii Thom		+		+		+	
P. nigricans (Bain.) Thom	+	+	+	+	+	+	
P. paxilli Bain.	+	+	+	+	+	+	S.s.
P. puberulum Bain.	+	+	+	+	+	+	*H.f.*
P. purpurogenum Stoll	+	+		+	+	+	*H.f.* C
P. purpurrescens (Sopp) Raper & Thom	+	+	+	+	+		
P. pusillum Smith			+	+	+	+	*H.s.;* S.s. Rab. S.
P. raciborskii Zal.	+	+		+	+	+	
P. restrictum Gil. & Abb.	+	+	+	+	+	+	*H.f.*
P. rolfsii Thom							Rab. S. Wal. S.
P. spinulosum Thom	+	+	+	+	+	+	Wal. S.; H.s.
P. tardum (?) Thom							Wal. S.
P. thomii Maire	+	+	+	+	+	+	*H.s.*
P. verruculosum Peyron.	+	+	+	+	+	+	
P. viridicatum Westl.		+					
P. waksmani Zal.	+	+	+	+	+	+	
Scopulariopsis brevicaulis (Sacc.) Bain.	+	+	+	+	+		

TABLE 2 (*Continued*)

Species	Source of Isolation						
	Soil	*Epac.*	*Leuc.*	*Lep.*	*Hib.*	*Dil.*	Other*
S. sp.	+						C
Sepedonium chrysospermum (Bull.) Fr.	+						
Dematiaceae							
Acrospeira asperospera (Cooke & Massee) Wilt.							Rab. S.
Alternaria fasciculata Cooke & Ellis						+	
A. geophila Dasz.			+				
Cladosporium herbarum (Pers.) Link	+	+	+	+	+	+	S.s.; Rab.
Dicoccum asperum Corda	+						C+
Diplococcium resinae (Corda) Sacc.	+						C
Humicola sp. (?)							C+
Monotospora daleae Mason		+			+		
Nigrospora sp.					+		
Pullularia pullulans (de Bary) Berkh.							*H.f.*
Stemphylium botryosum Wallr.	+						
S. sp.	+						
Torula sp. (?)	+			+	+		S.s.
Tuberculariaceae							
Fusarium neoceras Woll. & Rein.	+	+	+	+		+	C+
F. orthoceras App. & Woll.	+				+	+	*H.f.*
F. sp. (*elegans* series)		+					C+
F. sp. (*liseola* series)	+						C
F. sp. (*sporotrichiella* series)				+	+		C
F. sp. *A*		+			+	+	C+
F. sp. *B*				+			C
†*Spegazzinia* sp.					+		
Sphaeropsidales							
Aposphaeria sp. (?)	+	+	+	+	+	+	
Cystospora sp.		+	+		+		
Heteropatella sp. (?)			+				
Phomopsis sp.	+						
Pyrenochaeta sp.	+						
Unclassified							
Dark hyphal form	+	+	+	+	+	+	
Pale hyphal form	+		+				
Actinomycetales							
Streptomyces albus (Rossi-Doria em. Krain.) Waks. & Henr.		+	+				C±
S. erythreus (Waks.) Waks. & Henr. (?)					+		
S. olivaceus (Waks.) Waks. & Henr.	+	+					
S. sp. 6		+	+	+			C
S. sp. 7	+						

* Other habitats: *H.f.* = *Hypolaena fastigiata* R. Br.; *H.s.* = *Hibbertia sericea* R. Br.; *L.m.* = *Leptospermum myrsinoides* Schl.; Rab. = rabbit dung; Rab. S. = rabbit dung steamed for 3 min; S.s. = steamed soil; Wal. = wallaby dung; Wal.S. = wallaby dung steamed for 3 min; C = isolated with cellulose media; C+ = capable of decomposing cellulose.

† To be described.

the acid reaction (pH 4.8) of the medium employed. No special steps were taken to isolate members of the Actinomycetales, but three species of *Streptomyces* were identified and two species which could not be named also occurred. They were isolated regularly from soil plates, especially from those prepared with steamed soil.

All attempts to isolate *Azotobacter* gave negative results and Dr. Tchan advised that he had been unable to detect any acid-tolerant, nitrogen-fixing organisms. Of the 20 tubes inoculated with Frankston soil for the detection of *Clostridium,* only one showed any sign of gas production.

Since non-symbiotic bacterial fixation of nitrogen is negligible, the only means by which there could be a gain in soil nitrogen are by symbiotic fixation and addition in rain-water. No investigation was made on the possibility of nitrogen fixation by blue-green algae.

V. QUANTITATIVE ASPECTS OF THE FUNGAL FLORA

In this section consideration is given to the monthly variation in the number of fungi occurring in the free soil and in the rhizosphere of the five species of flowering plants. All the results presented here were obtained by means of the dilution-plate technique.

(*a*) *Significance of Variation between Monthly Populations*

Before considering the results in detail it is necessary to decide how much reliability can be placed upon the differences between the totals of each month. The apparent variation between monthly populations could have been due either to the fact that different samples were taken each month, i.e. to a variation between samples, or to a genuine variation with time which was independent of the variation between samples. Some information can be obtained for the free soil by comparing the counts obtained at monthly intervals with those from different samples of soil collected and plated on the same day.

Five samples of soil were collected from different parts of the general area in which soil and plants were usually taken, and these were plated by the dilution technique. The variability of the populations thus found was compared with that of the populations obtained at monthly intervals by calculating the variance ratio. The value found, 2.37, for 18 and 4 degrees of freedom, is not significant at the 5 per cent. level.

Hence differences among the populations found at monthly intervals are not significantly greater than those among the populations obtained from individual samples of soil collected from different places on the same day. Consequently, the apparent differences between the population of the soil at monthly intervals could be due merely to variation between samples of soil.

However, there were considerable differences in the moisture contents of the samples collected on the same day but there was no correlation between the number of fungi per gram of soil and the moisture content of these samples.

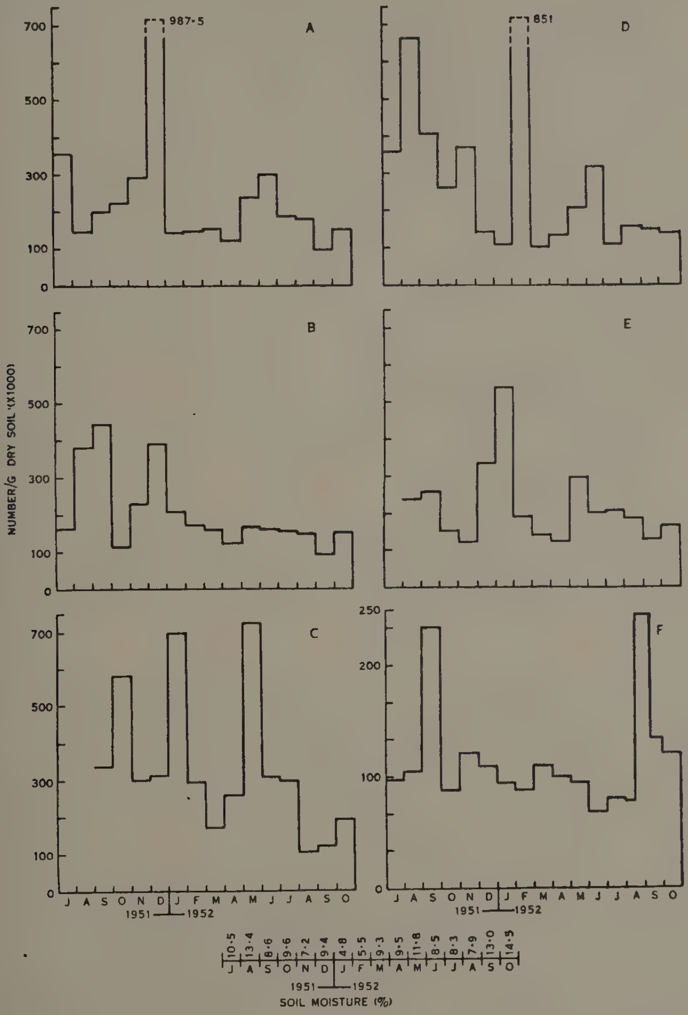


Fig. 1.—Variation in fungal population during the period July 1951 to October 1952. *A*, rhizosphere of *Epacris*; *B*, rhizosphere of *Leucopogon*; *C*, rhizosphere of *Dillwynia*; *D*, rhizosphere of *Lepidosperma*; *E*, rhizosphere of *Hibbertia*; *F*, root-free soil.

(*b*) *Variation in the Total Fungal Population*

The average populations obtained by the dilution-plate method at monthly intervals during a period of 16 months are shown in Figure 1; also shown is the percentage soil moisture recorded each month.

Correlation coefficients have been calculated in all cases for total fungal population and percentage of moisture in the soil. There was positive correlation, significant at the 1 per cent. level, between fungal numbers present in free soil and percentage moisture if the two very high values (Sept. 30, 1951 and Sept. 4, 1952) were omitted; when these two values were included correlation was no longer significant. Obviously, the high populations recorded in September of each year were not related to improved moisture conditions in the soil.

None of the species of higher plants showed significant correlation between total rhizosphere population and soil moisture. Moreover, whereas the correlation was positive between population of the free soil and soil moisture, that between rhizosphere population and soil moisture was always negative. Hence, whereas the soil population tended to increase with higher percentages of soil moisture, the populations of the rhizospheres apparently increased as the soil became drier. It is suggested that there is a range of moisture contents within which fluctuation has little effect upon the fungal population; if the soil moisture fell below this range, desiccation would limit fungal activity and lead to a diminution in numbers.

The fungal population of the free soil reached its highest level in September of each year of investigation. Most species of "host" showed a high rhizosphere population in December or January, but fluctuations in the rhizosphere populations of the five species did not conform to any common pattern.

(*c*) *Monthly Variation in the* R/S *Ratio*

The commonest method of numerically comparing the population of the rhizosphere with that of the free soil is by means of the *R/S* ratio, i.e. number of organisms per gram rhizosphere soil: number per gram free soil.

Clark (1947) has discussed the influence of water content on the magnitude of the apparent rhizosphere effect, pointing out that when the soil was comparatively dry the proportion of roots was higher in the "roots & soil" sample with which the original dilution was prepared. He suggested that some of the differences in the results of quantitative rhizosphere studies ascribed to the influence of age or conditions of growth might have been due to the character of the root samples employed. If this were so there should be some correlation between the *R/S* ratio and the moisture content of the soil at the time of sampling. In no case did the correlation coefficient between these two variables attain a significant value. Though the effect was statistically negligible, correlation was always negative so that the *R/S* ratio tended to rise as the moisture content of the soil declined. Therefore, the *R/S* ratio is an adequate means of expressing the rhizosphere effect, provided that gross differences in the proportion of roots to soil are avoided.

The R/S ratios for the five species of higher plants are shown in Figure 2.

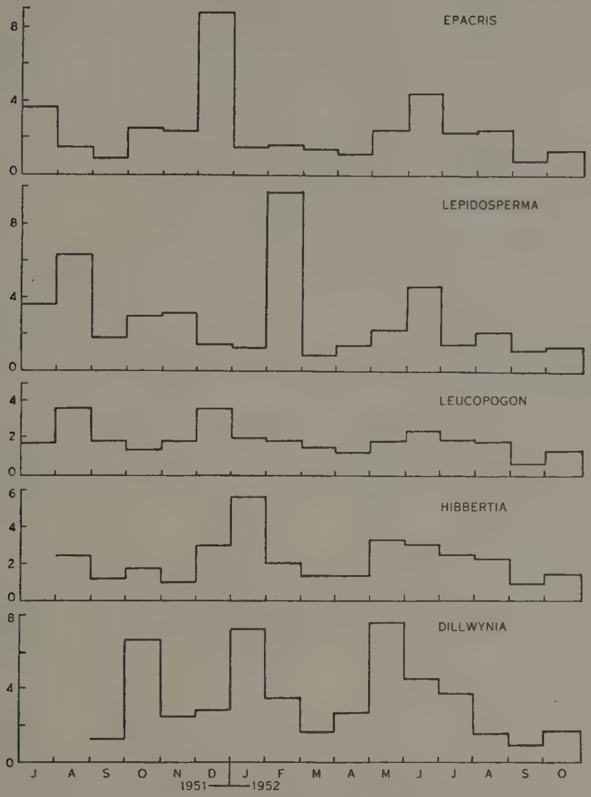


Fig. 2.—Variation in the R/S ratio of five species of flowering plants during the period July 1951 to October 1952.

The results obtained may be summarized as follows:

(i) The R/S ratio of *Epacris* was highest in December (8.9) and lowest in September 1952 (0.7).

(ii) The highest R/S ratio of *Lepidosperma* was recorded in February (9.7) and the lowest in March 1952 (0.9).

(iii) *Leucopogon* showed the lowest average ratio; the highest values (3.6) were recorded in September and December 1951.

(iv) The R/S ratio of *Hibbertia* was highest in January (5.6) and lowest in September 1952 (0.95).

(v) *Dillwynia* showed the highest average (3.0) and most variable R/S ratio.

During 1952 full notes were kept on the developmental phase of the host plant in an attempt to find if any relationship existed between the rhizosphere population and development of the host. Only for *Epacris* and *Leucopogon* were sufficient data obtained to permit any conclusions to be drawn. During the flowering period of *Epacris* the rhizosphere effect reached a maximum in the middle of flowering and there was a marked decline during the fruiting and subsequent vegetative phase. *Leucopogon* showed its greatest rhizosphere effect during the late bud and early flowering stages.

Table 3

DISTRIBUTION OF THE MOST ABUNDANT SPECIES OF FUNGI

Populations in thousands

	Soil	*Epacris**	*Leucopogon*	*Lepidosperma*	*Hibbertia*	*Dillwynia*
Average plate count	110.1	244.3 (2.4)	204.0 (1.9)	280.0 (2.5)	219.0 (2.0)	332.0 (3.0)
Absidia cylindrospora	2.8	1.4 (0.5)	6.7 (2.4)	5.9 (2.1)	1.1 (0.4)	1.3 (0.5)
Mortierella ramanniana	7.0	1.4 (0.2)	4.3 (0.6)	5.3 (0.8)	4.4 (0.6)	6.6 (0.9)
Pythium 'A'	4.6	9.7 (2.1)	4.9 (1.1)	14.6 (3.2)	1.1 (0.3)	1.7 (0.4)
Total Phycomycetes	14.4	12.5 (0.9)	15.9 (1.1)	25.8 (1.8)	6.6 (0.5)	9.6 (0.6)
Aspergillus fumigatus	38.5	17.4 (0.5)	32.6 (0.9)	48.7 (1.3)	50.0 (1.3)	86.4 (2.2)
Aspergillus sp. 6	11.0	9.7 (0.9)	7.1 (0.6)	8.7 (0.8)	7.0 (0.6)	19.9 (1.8)
Cladosporium herbarum	0.7	4.8 (6.8)	2.0 (2.9)	1.4 (2.0)	3.0 (3.8)	10.6 (15.0)
Trichoderma viride	3.4	5.1 (1.5)	1.4 (0.4)	7.8 (2.3)	4.2 (1.2)	9.6 (2.8)
Total	53.6	37.0 (2.4)	43.1 (1.2)	66.6 (1.6)	64.2 (1.7)	126.5 (5.4)
Penicillium adametzi	4.5	16.4	25.1	19.6	24.0	15.6
P. canescens	0.6	7.0	5.9	3.4	2.2	10.0
P. expansum	0.2	1.0	1.4	2.5	2.6	9.3
P. frequentans	2.0	14.4	3.3	9.2	7.4	10.6
P. godlewski	2.0	11.7	4.1	3.4	4.8	3.3
P. janthinellum	2.4	6.3	2.6	1.1	3.7	3.3
P. nigricans	0.9	11.7	6.9	14.6	3.1	7.3
P. restrictum	3.0	6.6	8.2	12.6	8.5	7.3
P. spinulosum	1.9	16.8	7.3	13.2	14.7	8.0
P. waksmani	2.3	14.4	10.2	10.6	14.9	7.6
Sclerotial penicillia	0.4	31.5 (79)	11.8 (29)	12.0 (30)	9.0 (22)	24.9 (62)
Total penicillia	20.2	137.8 (6.8)	86.8 (4.2)	102.2 (5.1)	94.9 (4.7)	107.2 (5.3)
Total, listed species	88.2	187.3 (3.4)	145.8 (2.2)	194.6 (2.8)	165.7 (2.3)	243.2 (3.8)
Total, other species	21.9	57.0 (2.7)	58.2 (2.7)	85.4 (3.9)	53.3 (2.4)	88.8 (4.0)

* *R/S* ratio in parentheses.

VI. Qualitative Aspects of the Fungal Flora

This section is concerned with the distribution of some of the more important species between the soil and the rhizosphere in order to show the qualitative differences that exist between the habitats. The results recorded in Table 3 were obtained from dilution plates; the "average population" was the average of the 16 monthly counts.

The 18 species listed constitute 69-80 per cent. of the total number of fungi per gram of soil, leaving only 20-31 per cent. to be accounted for by the other 77 species recorded from the soil or rhizosphere.

Individual consideration of the groups shows that some species were more abundant in the soil, while others were found more frequently in the rhizosphere. There was a fairly sharp distinction between these two groups in that species showing a preference for the rhizosphere of one plant usually showed a similar preference for the rhizospheres of the other plants that were studied.

The Phycomycetes were proportionately more abundant in the free soil; indeed, the actual numbers present were often higher than in the rhizosphere. Of this group, *Mortierella ramanniana* was the most abundant in the soil and also showed the strongest negative rhizosphere effect. Ascomycetes were not abundant enough nor of sufficiently wide distribution to be considered here.

Of the Fungi Imperfecti other than *Penicillium,* the species of *Aspergillus* were the most important and both were proportionately more abundant in the free soil than in the rhizosphere. *A. fumigatus* was the most abundant single species in both the free soil and the rhizospheres, but the *R/S* ratio did not attain the average value of any species of host plant.

The 11 species or groups of *Penicillia* made up 18.3 per cent. of the total population of the free soil, but 32.0 per cent. (*Dillwynia*) to 56.4 per cent. (*Epacris*) of the rhizosphere population. The sclerote-forming penicillia had extremely high *R/S* ratios, ranging from 22.5 (*Hibbertia*) to 79.0 (*Epacris*). Thus of the genera listed in Table 3 *Penicillium* was predominant in the rhizosphere.

In a study of the distribution of penicillia in Victorian soils, McLennan and Ducker (1951) recorded some species from all horizons of the Frankston soil while others were apparently restricted to one or two horizons. They isolated the sclerotial penicillia (*P. thomii, P. lapidosum, P. pusillum*) only from the A_0 horizon, and found that a simple selective technique was to pour malt extract agar at 60-80°C onto fragments of litter in a petri dish. The present study indicates that these species showed a marked association with higher plants.

Stapp and Bortels (1935) found that *P. thomii* was abundant on the litter of forest soils and that it was an active decomposer of tannins. It may be concluded that the sclerotial forms inhabit the litter because they are thus enabled to avoid the more rigorous conditions in the mineral soil. Adaptations to this habitat are seen in the formation of resistant sclerotes and the possible ability to utilize tannins. It is suggested that they do not penetrate deeply into the soil along the roots, but tend to occupy the soil-level region where, in species such as *Lepidosperma,* a good deal of moribund and dead material collects. Hence, the observed association is not a true rhizosphere effect.

VII. SOME PHYSIOLOGICAL ASPECTS OF THE MICROFLORA

(a) *Nutritional Requirements*

Work by Lochhead and Thexton (1947) showed that bacteria with relatively simple nutritional requirements existed in greater numbers in the rhizosphere than did organisms with more demanding requirements. An investigation to ascertain whether a similar effect exists in fungi was undertaken with the species isolated from the Frankston soil.

The seven media employed were similar to those described by Lochhead and Chase (1943), except in the following respects:

(i) The pH was adjusted to 4.6, the value found for the A_1 horizon.

(ii) Pantothenic acid (100 μg/l) was omitted from media *G* and *AG* because it was unavailable in Melbourne when the work was carried out. However, its omission was probably unimportant since Hawker (1950) pointed out that no filamentous fungi are known to require it.

Freshly isolated cultures of each species to be tested were grown on the seven media at 24°C and, at intervals of 1-2 days, measurements of linear growth were made in two directions at right angles. In addition, the relative amount of aerial growth and the degree of sporing were estimated by examining the colonies macroscopically and microscopically.

In the pioneer work on this subject Lochhead and his coworkers (Lochhead and Chase 1943; Lochhead and Thexton 1947) concerned themselves only with bacteria and estimated relative growth in the seven media on the basis of turbidity produced in liquid culture after 5 days incubation. The method used with fungi did not permit ready replication and the results were much less clear-cut than those obtained with bacteria.

Consideration of Table 4 shows that in the rhizosphere there was a higher percentage of fungi that gave maximum growth on media *B* and *A* than was present in free soil. In the soil, 27.1 per cent. of the total showed maximum growth on these two media; this was increased to 40-53 per cent. in the rhizospheres of the five species studied. Consequently there was a high *R/S* ratio (av. 4.0-4.7) in organisms with simple nutritional requirements, particularly the fungi producing maximum growth on the basal medium.

Conversely, the free soil contained a higher proportion of fungi with complex requirements (*AG* and *YS*). Medium *YS* was the most important single medium with respect to the proportion of species producing maximum growth on it and the percentage requiring it was higher in the free soil than in the rhizosphere. The percentages of fungi isolated from rhizosphere and free soil which required this medium were very much greater than the figures recorded by Lochhead and Thexton (1947) for bacteria (e.g. soil 51.8, cf. 11.1 per cent.; rhizosphere 27.4-48.4, cf. 2.5 per cent.). Recently, Rovira (1953) reported that 73 per cent. of free-soil bacteria needed media *S*, *Y*, or *YS* for maximum growth, and that the figure was increased to 86 per cent. of bacteria isolated from the rhizospheres of oats and clover. From Table 4 the proportion of fungi requiring the three media were 57.9 per cent. of the free soil population and 38.5-54.0 per cent. of the rhizosphere populations. In both free soil and rhizosphere the percentage of fungi producing maximum growth on media *G*, *Y*, and *S* was low; the three media together accounted for no more than 17.2 per cent. of the total.

TABLE 4

PERCENTAGE OF FUNGAL POPULATION GIVING OPTIMUM RESPONSE ON DIFFERENT MEDIA, AND THE CORRESPONDING R/S RATIOS

Medium	Soil	*Epacris*		*Leucopogon*		*Lepidosperma*		*Hibbertia*		*Dillwynia*	
	(%)	(%)	*R/S*	(%)	*R/S*	(%)	*R/S*	(%)	*R/S*	(%)	*R/S*
Average *R/S* ratio (plate count)			2.2		1.9		2.5		2.0		3.0
				Growth							
B	7.5	21.3	6.3	21.6	5.3	17.8	6.1	22.9	6.1	12.2	4.9
A	19.6	28.0	3.2	31.2	2.6	23.0	3.0	25.0	2.4	26.2	3.9
G	2.8	6.1	4.6	3.4	2.3	0.6	0.5	4.3	3.0	6.6	7.1
AG	12.2	6.1	1.1	5.1	0.8	4.6	0.9	4.4	0.7	8.2	2.0
Y	2.2	7.3	7.4	2.9	2.4	1.8	2.1	3.1	2.8	1.4	1.4
S	3.9	3.8	2.2	5.6	2.7	3.8	2.5	2.7	1.4	4.9	3.8
YS	51.8	27.4	1.2	30.2	1.1	48.4	2.4	37.6	1.5	40.5	2.4
				Sporulation							
B	6.0	17.1	6.4	8.2	2.5	8.7	3.7	10.0	3.3	7.2	3.6
A	29.3	44.2	3.6	38.0	2.1	31.0	2.7	40.2	2.7	27.7	2.9
G	10.3	1.0	0.2	3.0	0.5	2.8	0.7	2.8	0.5	3.9	1.1
AG	46.5	26.0	1.2	35.2	1.4	40.0	2.2	38.8	1.7	54.6	3.5
Y	4.4	7.8	3.9	9.8	4.0	10.8	4.9	2.7	1.2	3.6	2.5
S	—	—	—	—	—	—	—	—	—	—	—
YS	3.5	3.9	2.0	5.8	3.0	6.7	4.8	5.5	3.1	3.0	2.6

B: Basal medium (glucose + salts).
A: Basal medium + amino acids.
G: Basal medium + growth factors.
AG: Basal medium + amino acids + growth factors.
Y: Basal medium + yeast extract.
S: Basal medium + soil extract.
YS: Basal medium + yeast + soil extract.

The requirements for sporulation were different from those for vegetative growth. The percentage of fungi giving maximum response on media *B* and *YS* was much less important. Conversely, there was an increase in the percentages giving maximum response on medium *A* and a marked increase in the requirement for medium *AG;* these two media together accounted for 75.8 per cent. of the isolates from free soil and 70.2-82.3 per cent. of those from the rhizosphere. Hence it would appear that, for maximum sporulation, there is a strong requirement for amino acids, alone and with growth factors.

As a rule the *R/S* ratios of fungi requiring media *G* or *AG* for sporulation are lower than the average values, so that fungi with requirements for these substances are relatively suppressed in the rhizosphere. Conversely, the *R/S* ratios for fungi producing maximum sporulation on media *B* and *A* are above average. Thus, while the requirements of the general mycoflora for maximum sporulation differ from those for maximum growth, there is a pronounced stimulation in the rhizosphere of fungi requiring only simple substances for maximum sporulation, and in this respect there is a resemblance to the results obtained for mycelial growth.

(*b*) *Decomposition of Cellulose*

Some attempts were made to isolate bacteria and fungi capable of decomposing cellulose in order to find whether there was any difference in type or activity between those present in the free soil and in the root zone; the methods have been described in a previous section.

The technique used for testing cellulolytic ability was not entirely satisfactory because of the difficulty in detecting whether clearing of the medium had occurred. The organisms to be tested were plated on ammonium sulphate-cellulose agar (Fred and Waksman 1928) and inspected periodically for decomposition of cellulose. Results are presented in Table 2. No cellulose-decomposing bacteria were isolated in pure culture. In some instances the filter paper at the air-liquid interface softened and became pinkish brown in colour. When this material was examined in nigrosin mounts, two types of organisms were observed. Little reaction was noted in the deep tubes. Very occasionally some brown spots appeared on the submerged paper and from these was isolated a short, rod-shaped organism.

Actinomycete colonies were very abundant on the filter paper in the shallow tubes. Often the paper on which they grew was disintegrated and brownish in colour. A common form corresponded to *Streptomyces olivaceus.*

Sixteen species of fungi were isolated from cellulose plates or tubes; of these, six species were not obtained by any other technique, viz. *Dicoccum asperum, Diplococcium* sp., *Humicola* sp., *Scopulariopsis* sp., and two species of *Fusarium.* Of the 11 species tested for their ability to grow on a cellulose medium, all actually grew but only eight showed any signs of cellulolytic activity; the most active was *Humicola* sp. followed by *Dicoccum asperum.* Some of the forms isolated have been reported as decomposers of cellulose, e.g. *Chaetomium* sp., *Dicoccum asperum, Fusarium* sp., *Humicola* sp., and *Trichoderma viride.* Subsequently, *T. viride* was found to be by far the most abundant form on the decomposing litter.

Little direct information concerning the distribution of the species between free soil and roots was obtained, but some is available from the results of dilution plates. Of the forms with a proven capacity to decompose cellulose, *T. viride* was fairly evenly distributed between the soil and the rhizosphere. From Table 2 the *Fusarium* spp. seem to be more abundant on the roots and this was borne out by the fact that, during attempts to isolate *Pythium* and related forms from roots, a species conforming to the type here designated "*F. neoceras*" was obtained repeatedly.

(*c*) *Antibiotic Production*

Sixty-eight species of fungi and *Streptomyces* were tested for antibiotic activity against *Escherichia coli* and *Staphylococcus aureus*. The method employed has been described by McLennan and Ducker (1951).

Table 5 presents an analysis of the number of positive species from each habitat, and the percentage of total isolations from each habitat that gave a positive reaction.

TABLE 5

NUMBER AND PERCENTAGE OF ANTAGONISTIC SPECIES ISOLATED FROM FREE AND RHIZOSPHERE SOIL

	Species Antagonistic to *Esch. coli*		Species Antagonistic to *Staph. aureus*	
	No.	%	No.	%
Soil	10	11.1	13	20.7
Epacris	7	21.2	9	26.0
Leucopogon	8	17.7	9	16.6
Lepidosperma	7	13.6	10	27.1
Hibbertia	6	19.2	11	26.1
Dillwynia	4	11.8	7	18.5

Penicillium (8) and *Fusarium* (6) were the genera with the greatest number of species showing antibiotic properties, no other fungal genus possessed more than a single active species. Two species of *Streptomyces* were also active. Both the free soil and the rhizospheres possessed a greater number and percentage of fungi which were antagonistic to *Staph. aureus* than to *Esch. coli.* The number of antagonistic species was smaller in the rhizosphere than in the free soil, but the percentage of total isolates which were inhibitory was greater in the rhizosphere, i.e. the members of the antibiotic-producing species were present in large numbers there. In other sections of this account it has been shown that the two important antibiotic-producing genera, *Penicillium* and *Fusarium*, are more abundant in the rhizosphere than in the free soil; one species of the latter genus, *F. neoceras,* seemed to occur actually on the surface of the roots.

The fact that certain fungi can produce antibiotics in culture need not mean that they can perform a similar function in soil and Waksman (1952) considered the established facts to be too meagre for generalization on this topic.

VIII. DISCUSSION

The principal feature of the Frankston environment may be stated briefly as an acid, well-drained soil of sandy texture. Only small amounts of litter are produced and decomposition proceeds slowly. There is evidence that the fungal component of the microflora is dominant.

During the period of investigation, the fungal population of the root-free soil varied from 68,500 to 247,600, with an average of 110,000 per gram of oven-dry soil. The R/S ratios varied from 0.7-0.9 (min.) to 5.6-9.7 (max.), with the exception of *Leucopogon virgatus* (0.6-3.6); for this species, which has a very stout main root with few laterals, a rhizosphere population more than twice that of the free soil was rarely recorded. The values quoted here correspond with those observed for various crop plants.

Waksman (1927) quoted 18 genera of fungi as having a wide distribution throughout the temperate regions of the world; 12 of these were isolated from the Victorian soil. Obviously, so far as genera are concerned, the population of the Frankston soil has much in common with those of other temperate regions. From the aspect of fungal distribution, it is interesting to note the isolation of *Byssochlamys fulva,* which, although abundant in the soils of south England, is apparently absent from the United States. Also isolated was *Amphichaeta grevilleae,* which was recently described as a new species from Ceylon (Loos 1950). Of the 115 recorded species of fungi, 52 were isolated from both free soil and rhizosphere, a further 25 species were obtained only from the soil, and 27 from the rhizosphere. The remaining 11 species were found only in dung.

It is very noticeable that few species with a mucilaginous spore surface (Gloiosporae) were isolated; Burges (1950) has shown that slimy-coated spores are more readily washed down through the soil than are dry-coated spores. *Trichoderma* was isolated frequently from both habitats but six species of Coelomycetes were obtained from the roots compared with only three from the free soil. *Fusarium* was more common on the surface of the roots, as was *Oospora* and probably *Gliocladium.* Thus, while the comparative absence of members of the Gloiosporae indicated that "washing down" might be an important factor in determining their distribution under natural conditions, there was little to indicate that some of them might be retained in the root zone; *Fusarium* was the only genus for which there was reasonable positive evidence for such retention.

In a previous section it was pointed out that *Aspergillus fumigatus* was the most abundant single species in both the free soil and the rhizosphere, but that it was relatively inhibited in the rhizosphere; the latter observation was true also for *Aspergillus* sp. 6. Similarly, the three species of Phycomycetes considered in detail (*Absidia cylindrospora, Mortierella rammaniana, Pythium* sp. *A*) were predominantly members of the free-soil mycoflora. The same was probably true of the four other species of *Mortierella* that were isolated.

Conversely, the presence of all the penicillia was stimulated in the rhizosphere and, with *Fusarium,* they were the characteristic forms of this habitat. Garrett (1951) has pointed out that both these genera form "dense but restricted colonies immediately around the substrate and scarcely extending into the surrounding soil". Fungi with such a growth habit are admirably adapted to existence on the root surface and in the rhizosphere.

None of the more abundant species was entirely absent from either the rhizosphere or the free soil, though at times the population of a particular species in one habitat or the other was very low. Difficulties were encountered when an attempt was made to compare these results with the qualitative rhizosphere effects reported by various workers. Reasons for this include the comparatively small number of isolates taken in most cases, and identification only to the level of genus. This is particularly important when genera with large numbers of species are considered for there is no reason to suppose that all species of a particular genus are physiologically identical, and it is upon the physiological potential of a species that preference for a particular habitat must depend.

Timonin (1941) found that, of 19 genera isolated from the free soil or rhizosphere of flax, nine occurred in both habitats, while 10 were confined to the rhizosphere. There were no similarities between the genera found exclusively in the rhizosphere by Timonin and those predominating in the rhizospheres of the native plants at Frankston.

It is suggested that the general fungal population is capable of rapid exploitation of suitable conditions of substrate and moisture. Evidence in support of this suggestion is seen in the marked, but brief, increase in the population that occurred in September of each year. It is also suggested that the rhizosphere, in an environment such as that provided by the Frankston soil, is often no more favourable for microbial activity with respect to moisture relations than is the free soil.

The results can be summarized by saying that the rhizospheres of the five species of native plants were characterized by larger fungal populations than the free soil, dominated by *Penicillium* spp., and with *Fusarium* spp. as an important component. The population was probably more active antibiotically than was that of the free soil, but there was no evidence of a significantly larger population of cellulose decomposers. Fungi having simple requirements for vegetative growth and sporulation were relatively stimulated in the rhizosphere although the largest single group in both habitats required a complex medium.

IX. Acknowledgments

It is a pleasure to acknowledge my indebtedness to Professor J. S. Turner for the provision of financial assistance and for criticism of this paper in draft, and to Associate Professor E. I. McLennan for advice during the investigation, in addition to criticism of the manuscript.

X. References

Burges, A. (1950).—The downward movement of fungal spores in sandy soil. *Trans. Brit. Mycol. Soc.* **35**: 142-7.

Clark, F. E. (1947).—Rhizosphere microflora as affected by soil moisture changes. *Soil Sci. Soc. Amer. Proc.* **12**: 234-6.

Cunningham, A. (1947).—"Practical Bacteriology: An Introductory Course for Students of Agriculture." (Oliver & Boyd: Edinburgh.)

Curie, J. H. (1931).—Method for the study of *Azotobacter* and its application to fertility-plot soils. *Soil Sci.* **32**: 9-23.

Fred, E. B., and Waksman, S. A. (1928).—"Laboratory Manual of General Microbiology." (McGraw-Hill: New York.)

Garrett, S. D. (1951).—Ecological groups of soil fungi: a survey of substrate relationships. *New Phytol.* **30**: 149-66.

Hawker, L. E. (1950).—"Physiology of Fungi." (Univ. of London Press: London.)

James, W., and Sutherland, Marjorie L. (1939).—The accuracy of the plating method for estimating the numbers of bacteria and fungi from one dilution and from one aliquot of a laboratory sample of soil. *Canad. J. Res.* C **17**: 97-108.

Lochhead, A. G., and Chase, F. E. (1943).—Qualitative studies of soil microorganisms. V. Nutritional requirements of the predominant bacterial flora. *Soil Sci.* **55**: 185-95.

Lochhead, A. G., and Thexton, R. H. (1947).—Qualitative studies of soil microorganisms. VII. The "rhizosphere effect" in relation to the amino acid nutrition of bacteria. *Canad. J. Res.* C **25**: 20-6.

Loos, C. A. (1950).—*Amphichaeta grevilleae* n. sp., on *Grevillea robusta* seedlings. *Trans. Brit. Mycol. Soc.* **33**: 40-2.

McLennan, Ethel I., and Ducker, Sophie C. (1951).—The description and distribution of the species of *Penicillium* Link in some Victorian soils. *Proc. Roy. Soc. Vict.* **64**: 10-71.

Munsell, A. H. (1948).—"Munsell Soil Color Charts." Regular Form. (Munsell Color Company, Inc.: Baltimore.)

Pendleton, R. L., and Nickerson, D. (1951).—Soil colors and special Munsell soil color charts. *Soil Sci.* **71**: 35-43.

Piper, C. S. (1950).—"Soil and Plant Analysis." (Hassell Press: Adelaide.)

Rovira, A. D. (1953).—Some quantitative and qualitative aspects of the rhizosphere. First Aust. Conf. Soil Sci.: Adelaide, 1953.

Stapp, C., and Bortels, H. (1935).—Mikrobiologische Untersuchungen über die Zersetzung von Waldstreu. II. Tanninzersetzende Mikroorganismen in der Waldstreu. *Zbl. Bakt.* (II) **93**: 45-56.

TCHAN, Y. T. (1952).—Studies in nitrogen-fixing bacteria. II. The presence of aerobic, non-symbiotic, nitrogen-fixing bacteria in soils of the Sydney district. *Proc. Linn. Soc. N.S.W.* 77: 92-7.

TIMONIN, M. I. (1941).—The interaction of higher plants and soil micro-organisms. III. Effect of by products of plant growth on activity of fungi and actinomycetes. *Soil Sci.* 52: 395-413.

WAKSMAN, S. A. (1927).—"Principles of Soil Microbiology." 1st Ed. (Williams & Wilkins Co.: Baltimore.)

WAKSMAN, S. A. (1952).—"Soil Microbiology." (Wiley: New York.)

WARCUP, J. H. (1950).—The soil-plate method for isolation of fungi from soil. *Nature* 166: 117.

WARCUP, J. H. (1951).—The ecology of soil fungi. *Trans. Brit. Mycol. Soc.* 34: 376-99.

WHINCUP, SYLVIA (1944).—Superficial sand deposits between Brighton and Frankston, Victoria. *Proc. Roy. Soc. Vict.* 56: 53-76.

CORRIGENDUM

VOLUME 1, NUMBER 2

Plate 5; Figures 1 and 2 should read 2 and 1 respectively.

THE LEAF ANATOMY OF AUSTRALIAN MEMBERS OF THE GENUS *ATRIPLEX*

I. ATRIPLEX VESICARIA HEWARD AND A. NUMMULARIA LINDL.

By R. F. Black*

(*Manuscript received August* 2, 1954)

Summary

These two species are shown to have a closely similar leaf anatomy, and this is fully described with relevant notes on all the minor points of difference.

In discussion, the origin and development of the lamina are compared with other plant groups. The autecological significance of the vesicular hairs is also briefly considered from an anatomical point of view. Brief comments are made on the water-storage properties of the hypodermal layer. The widespread occurrence of the 'Kranz' type of assimilatory tissue (concentric to the xylem of the leaf veins) in the Australian species of *Atriplex* is noted. The need for further investigations on the thick-walled phloem elements and bundle sheath cells is stressed. A taxonomic significance is suggested for the peculiar ventral development of the midrib in both species.

I. Introduction

Anatomical investigations were commenced as a basis for studies on the water relations of the leaves, including the role played by the vesicular hairs, as they affect water uptake or loss by the epidermis. The peculiar anatomy, and the variations of it found within the genus, proved to be of great interest from an ecological viewpoint. Furthermore, many of these variations suggested the possibility of indicating phylogenetic relationships within the genus. Hence the work has been extended.

The present aim in this series is to arrange the Australian species in groups of similar leaf anatomy, and to present papers on each of these groups, together with relevant notes of ecological and taxonomic importance. Owing to the length of time which will be necessary to examine all species, it is anticipated that the groupings adopted, particularly in the early papers, will be to some extent tentative.

The genus is ideally suited to comparative studies of ecological anatomy for the following reasons. Firstly, its members are found in a wide variety of habitats, which include extreme examples of xerophytic and halophytic ones. Secondly, the genus possesses marked variations in the anatomical structure of the leaf. The qualitative aspects of these changes, which may at times correspond fairly closely to the naturally occurring environment, are usually firmly controlled by genetic factors. For this reason comparative studies of leaf anatomy can be of great assistance in the taxonomy of the group.

---

* Botany Department, University of Sydney.

The modifying effects of the environment, however, are often considerable, but usually of a more quantitative nature. Thus we may find big increases in cell elongation in many species brought about by a highly saline substratum. Also, low nitrogen levels, high light intensities, or very arid conditions usually bring about a big increase in density of epidermal hairs. It is not intended to deal with the above types of modifications or their causes in this series, except in so far as they may be of significance in considering ecads of a species found naturally in the field, or of variations found to be caused by seasonal conditions or the positions of the leaves on the plant. Also, to increase the validity of all anatomical and morphological descriptions, only specimens obtained from the field will be examined, unless otherwise stated.

The interrelationships of the various Australian species of the genus *Atriplex* have been carefully worked out by Aellen (1938), Anderson (1930), and many other workers, mainly on characteristics of the fruiting bracteoles, the seed, and the general morphology of the plant. As far as is known, no serious attempt has ever been made at a comparative study of leaf anatomy of the Australian species. It is felt that information of the latter type will be of value in clarifying many of these interrelationships, as fruit* characteristics can be confusing. For example, the fruit of *A. angulata* Benth. and *A. stipitata* Benth. can easily be confused from descriptions, even though the two species are by no means closely related. They can, however, be readily and distinctly separated by leaf characteristics, including anatomical distinctions. On the other hand, the typical appendaged bracteoles of *A. vesicaria* are quite distinct from those of *A. nummularia*. The leaf forms of typical specimens are also quite distinct, the leaves of *A. nummularia* being usually large, orbicular, and distinctly petiolate, while those of *A. vesicaria* are smaller, more oblong, and with no marked petiole. Thus the phylogenetic significance of their closely similar leaf anatomy is of great interest, but a full appraisal of this feature will have to wait on further anatomical information from other species. A point here perhaps worthy of note is that bracteoles without appendages can sometimes be found atypically on *A. vesicaria* plants. Furthermore, specimens† of *A. vesicaria* have been seen with the leaf form approaching that of *A. nummularia* in shape, but never in size, and with fruiting bracteoles typically without appendages.

The nomenclature used throughout this series will be as far as possible that adopted by Black (1948). All text figures are drawn with the aid of a camera lucida. The information set out in this paper has been obtained entirely from specimens collected in New South Wales.

* In this series Winkler's (1939) definition of fruit (product of gynoecium together with any accessory parts that may be associated with it in development) is adopted.

† Fowler's Gap collection, Herbarium, University of Sydney.

II. Description

(*a*) *Early Ontogeny and Histogenesis*

The leaf primordium commences as a small group of cells flattened along the stem apex, and semicircular in transverse section. It consists of a distinct dermatogen, and an inner region of an indefinite number of meristematic cells. Immediately on formation, the dermatogen of the free surfaces commences to bud off vesicle initials.

At the same time as the earliest differentiation of a few protoxylem elements in the central region and when the free portion of the leaf primordium is 0.2-0.3 mm long, the marginal meristems commence to develop from the points of the semicircle. These meristems consist of an outer strip of marginal initials which give rise to the ventral (adaxial) and dorsal (abaxial) dermatogens by anticlinal divisions, and an inner strip of submarginal initials which produce internal layers 1 and 4 by anticlinal divisions, and internal layer 2 by periclinal divisions (Figs. 1, 2; Plate 1, Figs. 1, 3). Internal layer 3 is produced by periclinal divisions of the dorsal derivatives of the submarginal initials (approx. 1-4 cells away from the initials). The meristematic cells of the six plate meristems so formed continue to divide by anticlinal divisions, and it is probable that the bulk of the expansion of the young lamina takes place by this intercalary growth.

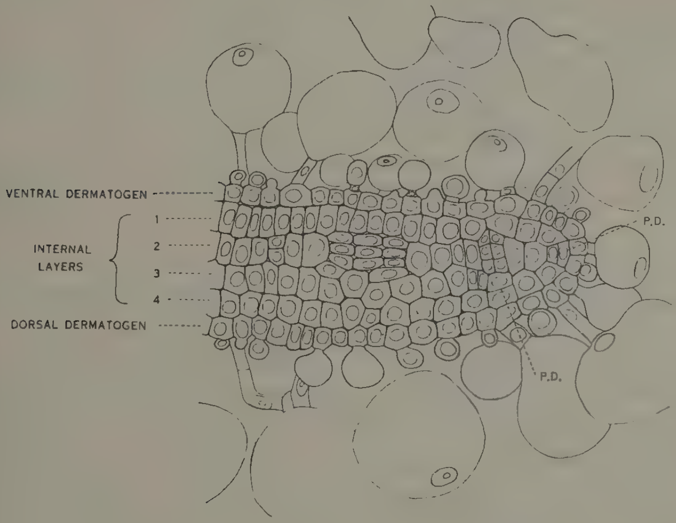


Fig. 1.—Transverse section of primordial lamina of *A. vesicaria*, showing the separate origins of internal layers 2 and 3 by periclinal divisions (*P.D.*) of the submarginal initial and a dorsal derivative. × 330.

As the meristem spreads out, divisions parallel to the plane of the lamina occur in the second internal layer at points where the major lateral veins will be (Plate 1, Figs. 1, 2, 3), but except for these interruptions, the six-layered stage is quite extensive, particularly in rapidly growing leaves (Fig. 1). At this stage, also, many vesicular hairs are complete and nearing maturity, and beginning to form a dense protective layer around the young leaf. Further periclinal divisions may occur in internal layer 4 near the midrib (Plate 1, Fig. 3), giving rise to an extra layer of hypodermal cells in this part of the leaf.

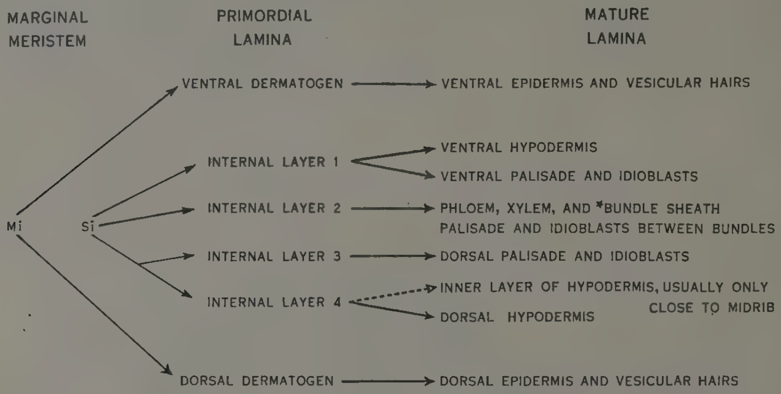

MARGINAL MERISTEM
PRIMORDIAL LAMINA
MATURE LAMINA
VENTRAL DERMATOGEN
VENTRAL EPIDERMIS AND VESICULAR HAIRS
INTERNAL LAYER 1
VENTRAL HYPODERMIS
VENTRAL PALISADE AND IDIOBLASTS
Mi
Si
INTERNAL LAYER 2
PHLOEM, XYLEM, AND *BUNDLE SHEATH
PALISADE AND IDIOBLASTS BETWEEN BUNDLES
INTERNAL LAYER 3
DORSAL PALISADE AND IDIOBLASTS
INTERNAL LAYER 4
INNER LAYER OF HYPODERMIS, USUALLY ONLY CLOSE TO MIDRIB
DORSAL HYPODERMIS
DORSAL DERMATOGEN
DORSAL EPIDERMIS AND VESICULAR HAIRS

Fig. 2.—Schematic representation of tissue differentiation in the leaf. *Mi*, marginal initials; *Si*, submarginal initials.

A slightly later stage shows divisions at all points in internal layer 2 where veins will occur, and also the earlier initiated veins complete with xylem, phloem, and bundle sheath. In at least these earlier-formed and larger veins it appears that some of the bundle sheath cells are derived from layers other than internal layer 2. Between veins the lamina is still only six-layered.

Subsequent to these changes (see Fig. 2), internal layer 1 divides periclinally to produce the ventral hypodermis and ventral palisade tissues. Internal layer 3 differentiates directly into palisade tissue, and internal layer 4 forms the dorsal hypodermis. The hypodermal and epidermal cells commence to vacuolate, and the guard cells differentiate. At this stage, when also all the veins and their sheath cells are clearly differentiated, and druse-containing idioblasts are quite large, the meristematic palisade cells are still actively dividing.

The above description fits equally well both species of *Atriplex* herein dealt with.

(*b*) *Epidermis and Vesicles*

It is generally true that the epidermal cells of both species are thin-walled (Fig. 3), particularly in comparison with certain more mesophytic species of *Atriplex* (e.g. *A. spinibractea* R. H. Anderson). The cells always appear clear of any inclusions, except a normal protoplast, and chloroplasts are present only in the guard cells. In surface view the epidermal cells are more or less straight-sided, and distinctly domed on the outer surface. The cuticle is so thin as not to be normally visible under the microscope. The stomates are simple, randomly arranged, and not sunken in any way (Fig. 3). The stomatal frequency is approximately the same on both the dorsal and ventral surfaces.

---

* In the larger veins, some of the sheath cells may be derived from periclinal divisions of internal layers 1 and 3.

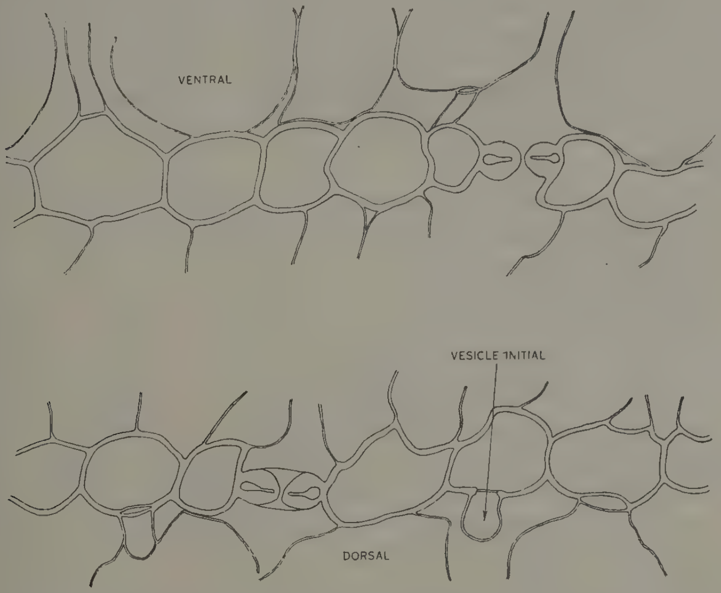


Fig. 3.—Transverse section of the ventral and dorsal epidermis of a mature leaf of *A. vesicaria*, showing a portion of the vesicular tissue to the outside, and parts of the hypodermal cells to the inside. × 410.

An important feature of the epidermal cells, and one which, on *a priori* grounds appears to be correlated with their characteristics of a thin cell wall and a thin cuticle, is the fact that they form the parent tissue of the vesicular hairs which are so abundant in both species. These hairs appear to originate as "blowouts" from the epidermal cells (Fig. 1; Plate 1, Fig. 1), the first division cutting off the vesicle initial (Plate 2, Fig. 1). A stalk cell may be formed by a subsequent division of this initial (Plate 2, Fig. 2), or the initial may enlarge directly to the ovoidal vesicle which at maturity is usually 0.15-0.20 mm long (Plate 3, Figs. 4, 5). Generally the vesicles are either shortly stalked with one cell, or the stalk may be long and consist of up to three cells. This process of vesicle initiation commences from the dermatogen of the earliest stages of the leaf primordia and stem apices, and apparently continues right through the ontogeny of the leaf up to the onset of senescence. It is not uncommon to see vesicle initials in mature leaves (Figs. 3, 4), and much more frequent on such leaves are young developing vesicular hairs pushing up under the older mature vesicles.

Under field conditions, the vesicular tissue is always several vesicles in thickness, and by the time the leaves have emerged from the bud, usually most of the outer vesicles have collapsed because of a slow loss of vacuolar water through the extremely thin cell wall and cytoplasm. While the vesicles are turgid they are tightly packed and pressing one against the other. The walls fuse very firmly in circular patches under this pressure. Because of the additional outward force of the younger developing vesicles, it appears that some of the outer vesicles are actually parted from their stalks, but remain in sufficiently intimate contact with other vesicles through wall fusion for them to stay turgid for some time while conditions permit.

As the young leaves emerge from the bud and expand in area, the mature and fused vesicles, which form the outer layers, are stretched in all directions of the plane of the blade. The areas of fusion remain firm, and the cell walls are stretched out into thin films (Fig. 4) with frequent striations or stretch marks which give the resulting structure a crystal-like appearance in surface view (Plate 2, Figs. 3, 4; Plate 3, Figs. 2, 3). When observed under oblique surface lighting, the film has a coloured oily appearance because of interference effects. It is this fusion, and the resulting formation of stretched films, that under certain conditions gives a rather smooth and shiny surface to the vesicular tissue. There are usually, however, enough raised clumps of empty fused vesicles and more or less unattached empty vesicles to give the surface a matt or mealy appearance.

The depth to which the vesicular tissue is deflated varies widely according to the prevailing environmental conditions. Plants grown on the coast under glass commonly have loosely packed turgid vesicles right to the surface in young leaves (Plate 3, Figs. 4, 5). Under field conditions, however, there is usually at least a single layer of empty and stretched vesicles at the surface, even in the youngest leaves which have emerged from the bud. Fresh specimens have been observed in the field from which the vesicular tissue could be peeled with needles without any release of free water. In these leaves, which are only found during exceptionally arid periods, all the vesicles appeared to be largely empty of vacuolar water, although those nearest the epidermis were not completely collapsed. However, in field specimens under normal conditions, probably most of the vesicles adjacent to the epidermis are fully turgid.

In certain specimens, where partially collapsed vesicles could be observed, the frequent occurrence of air bubbles within the vesicles was noted (Plate 2, Fig. 3). This explains how the inner vesicles would dry out under severe conditions, without collapsing completely.

The number of vesicles produced per unit of leaf area, or per unit number of epidermal cells, and hence the thickness of the vesicular tissue, varies widely according to the environmental conditions. Generally speaking, the more arid the environment of the developing leaf, the greater is this thickness. However, this environmental change also normally produces a smaller leaf. Thus we usually find in field specimens that these two quite distinct structural characteristics are closely correlated. They are, nevertheless, distinct, because firstly, the cell size of the small leaf is always approximately the same as that of the large leaf under normal field variations, and secondly, the two properties may be made to vary independently under artificial conditions.

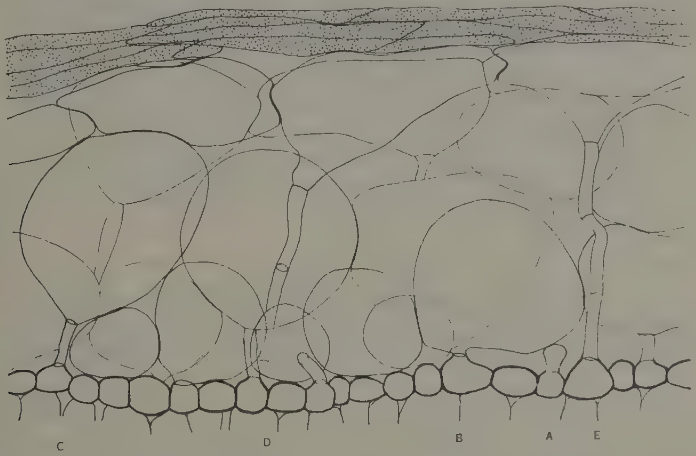


Fig. 4.—Cross section of heavily developed, segmented vesicular layer on a mature leaf of *A. vesicaria.* The surface layer of stretched, deflated vesicles shown by stippled area. *A*, a vesicle initial; *B*, a mature turgid one-celled vesicular hair; *C*, as with *B*, but with one stalk cell; *D*, three-celled and *E*, four-celled vesicular hairs. × 165.

This correlation can be shown often in bushes of *A. vesicaria*, where large "shade" leaves can sometimes be compared with much smaller "sun" leaves (Fig. 5). Also rain often produces a new growth of large leaves which can be compared with an older growth of small leaves, and vice versa. The correlation, though present, is not so marked in *A. nummularia.* In this species the vesicular tissue on each surface is usually from one-half to two-thirds of the thickness of the mesophyll, and approximately the same thickness on both surfaces. The vesicular tissue of *A. vesicaria* is normally somewhat thicker than this, and although commonly the layers are of equal thickness on both surfaces, specimens are found where the dorsal vesicular tissue can be as much as twice the thickness of the ventral.

A striking and fairly consistent difference between the appearances of the leaves of the two species is the smoothness and surface sheen of the vesicular film on *A. nummularia* leaves, as contrasted with the mealy, and sometimes segmented, surface characteristic of *A. vesicaria*. In a surface view of a typical leaf of *A. nummularia*, it is often difficult to pick out any individual vesicle which is not intimately fused with neighbouring vesicles, and kept near the general level of the layer. Thus when the surface film is formed (Plate 3, Fig. 6), it is more or less continuous and lies close to the underlying two to three layers of commonly turgid vesicles. With *A. vesicaria*, on the other hand, leaves are seen in all stages, from those possessing some surface sheen (Plate 3, Fig. 2), through those with a uniformly matt or mealy surface though sometimes tending to become scaly, to those with an almost white surface cut up into well-defined segments (Plate 3, Fig. 3). The common factor here appears to be the higher and more prolonged production of vesicular hairs in this species.

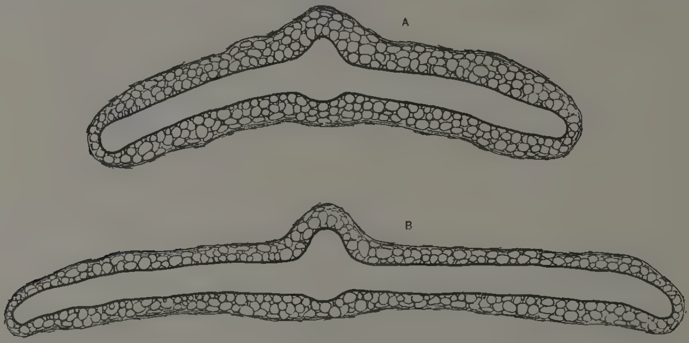


Fig. 5.—Transverse sections of typical "sun" and "shade" leaves from a male plant of *A. vesicaria*. Both leaves are mature and approximately the same age. *A*, "sun" leaf, 4 mm wide, 8 mm long; *B*, "shade" leaf, 5.5 mm wide, 16 mm long.

Thus the older vesicles are pushed up, sometimes in aggregates and sometimes singly, and spread about by the younger developing vesicles. Here they dry out and form the mealy surface. These scales, however, remain firmly fused to the turgid vesicles below. Segmentation occurs when a late increase in leaf size, or a progressive shrinkage of the dead vesicle walls, splits the older, empty, and fused vesicles along fissure lines all over the leaf. These fissures are filled by the younger turgid vesicles from below. The segments themselves usually consist of two to three layers of flattened and fused vesicles, which overlie two to three layers of younger turgid vesicular hairs.

(*c*) *Mesophyll and Vascular System*

The vascular system of the leaves of both *A. nummularia* and *A. vesicaria* is markedly reticulate. The anastomoses of the smaller veins cut off small vein islets of various shapes and sizes. Almost invariably each vein islet is further supplied with at least one shortly branching vein ramifying completely through the vein islet. Two layers of assimilatory tissue are concentric about the xylem of the veins (Fig. 6). The inner layer is a chlorenchymatous bundle sheath, consisting of thick-walled cells densely packed with starch-containing chloroplasts and with no intervening air spaces. These walls consist of a highly hydrated form of cellulose, as can be seen by their marked decrease in thickness in dehydrated sections. The phloem always lies open to the outermost concentric tissue (Fig. 6).

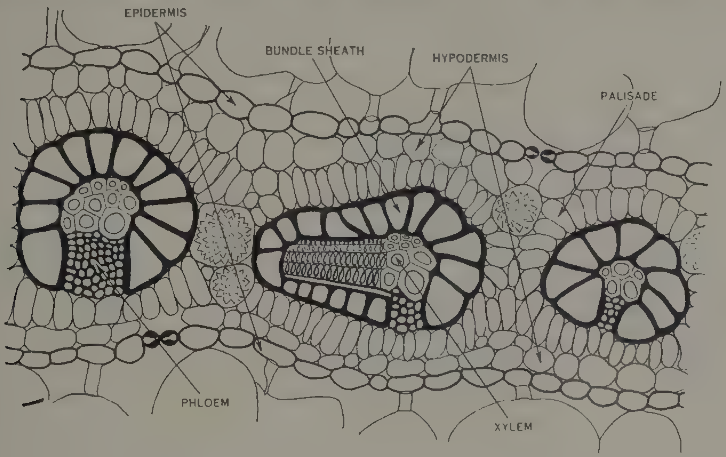


Fig. 6.—Transverse section of the lamina of a leaf of *A. vesicaria.* The centre vein shows in longitudinal section, a short lateral extension terminating within a vein islet. The full extent of the vesicular tissue is not shown. × 205.

This latter tissue is the palisade mesophyll, which consists of small, thin-walled cells with many intervening air spaces. They contain many chloroplasts, but in a much reduced density to that of the bundle sheath cells. These chloroplasts contain little or no starch. The palisade cells radiate out from the centre of the vein, except where the lateral cells may be distorted somewhat towards the ventral or dorsal surfaces. These lateral cells usually abut on to those of the adjacent bundle, although commonly large cells containing a calcium oxalate druse lie between the bundles. Similar idioblasts are often a feature of other parts of the palisade tissue. In some specimens the ventral palisade cells may be noticeably longer than the dorsal.

The outermost tissue of the mesophyll, which lies between the epidermis and the palisade cells, consists of thin-walled hypodermal cells. The ventral hypodermis invariably consists of a single layer of cells. The dorsal hypodermis consists of two layers at least within 1 mm or so from either side of midrib, the rest of this tissue then being a single layer. However, the two-layered portion in many specimens may be seen to extend more or less irregularly for up to two-thirds of the distance from the midrib to the leaf margin.

The hypodermal cells, as shown in Figure 6, are of a size most commonly met with in specimens of both species. However, occasionally they are seen to be much larger than these, and this expansion is always at right angles to the plane of the leaf. In such cases they often take the form of another palisade tissue, but they nevertheless remain quite distinct from the chlorenchymatous palisade cells.

In *A. vesicaria,* increases in volume of the hypodermal cells have been induced under artificial conditions by growing the plants in a highly saline substratum. This salt succulence develops after the leaf has expanded to its full size, and is thus a product of salinity, and the age of the leaf. It is almost entirely the result of expansion of the hypodermal tissues.

Although the above phenomenon is doubtless operative under certain field conditions, the hypodermal enlargement sometimes met with in field specimens of both species appears to be most commonly controlled purely by genetical factors. This is shown firstly, by the intermingling of such forms among more typical specimens, and secondly, by the occurrence in these forms of associated morphological distinctions not characteristic of salt-induced succulence. Examples are changes in leaf shape (a markedly linear leaf in one known form of *A. vesicaria*), and also sometimes a corresponding reduction in the thickness of the vesicular layers, which largely cancels out the succulent effect of the enlarged hypodermis.

The hypodermal cells are highly vacuolated from an early stage in the ontogeny of the leaf. Occasionally in some specimens a very few widely scattered chloroplasts may be found in some of these cells. Large druses also occur in other isolated cells, but these are invariably more common in the idioblasts of the palisade tissue. Smaller crystalline inclusions are frequent in the hypodermal cells of *A. nummularia.* Very large air spaces occur between cells underneath the stomates (Fig. 6).

(*d*) *Midrib, Petiole, and Leaf Trace*

In both species a single leaf trace arises from the stele of the stem at a point 1-2 mm below the lowest point of junction of the petiole and the stem (Fig. 7*A*). The leaf trace in the stem and the petiole is divided into a number of distinct vascular bundles, the number varying (even in the same trace) from three to eight. The leaf trace remains open in the proximal end of the petiole (Fig. 7*B*), but at a point approx. 4 mm from the stem it closes, forming a hollow stele with a small thick-walled pith (Fig. 7*C*). Thus the type of leaf trace shown by a section cut at the distal end of the petiole depends entirely on the petiole length of the specimen examined. *A. nummularia* normally has a petiole length of 4-10 mm, and so the distal section in this species normally shows a closed trace of the type illustrated in Figure 7*C*. The petiole length of *A. vesicaria* is usually only 1-2 mm long, and so in this species the petiole leaf trace is always open, the trace closing only after it has entered into the blade of the leaf.

At a point along the petiole of both species, thick-walled chlorenchymatous bundle sheath cells commence to appear on either side of the leaf trace (Fig. 7*C*). After the closing of the stelar gap, the leaf trace or midrib comes to consist of two large apposed bundles, one in a ventral position, and a somewhat larger one in a dorsal position (Fig. 8), the latter being often subdivided into two or three distinct, smaller vascular bundles. A band of bundle sheath cells lies to either side of these bundles, leaving the phloem of each bundle open to the dorsal and ventral collenchyma. Lateral veins split off both dorsal and ventral bundles, those from the ventral bundle turning through 180° before becoming aligned in the lamina.

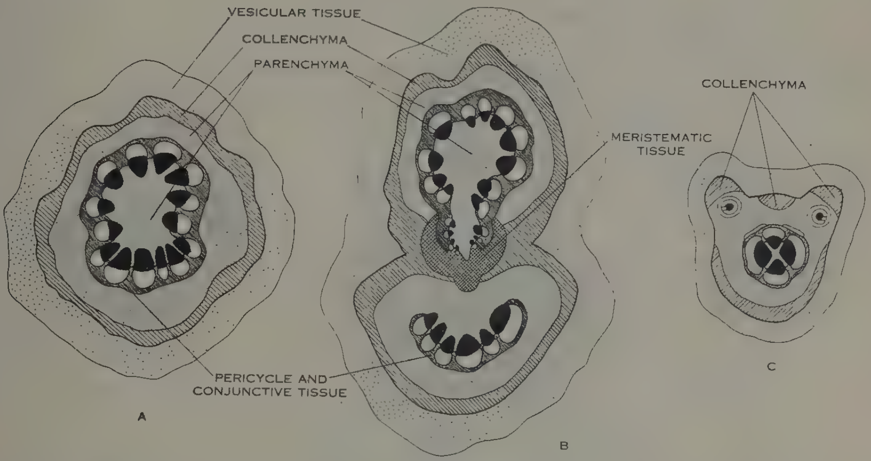


Fig. 7.—Drawings showing the origin and development of the leaf trace in a leaf of *A. nummularia*. *A*, cross section of stem cut 1-2 mm below the lowest point of junction of the petiole and stem; *B*, cross section of stem at the junction of the petiole and stem; *C*, cross section midway along the petiole, at a point 4 mm from its junction with the stem. (Vesicular tissue is coarsely stippled; parenchyma, finely. Collenchyma is lightly cross-hatched; pericycle and conjunctive tissue, heavily. Meristematic tissue of the axillary bud in *B* is doubly cross-hatched. The phloem and chlorenchyma tissues are left blank.)

Transverse sections cut progressively along the blade towards its tip show the relatively decreasing importance of the ventral bundle, until it finally disappears, usually about two-thirds of the way along the midrib. The ventral gap in the bundle sheath, now above the xylem of the dorsal bundle, normally persists until it eventually closes near the leaf tip. However, in some of the specimens of *A. vesicaria* examined, the ventral gap closes or partially closes before the ventral bundle disappears. Thus in some transverse sections of these specimens cut half way along the leaf, either the palisade tissue may be continuous and separate the ventral phloem from the ventral collenchyma (Fig. 8), or the bundle sheath cells may also be more or less continuous. Often in the latter case, one or two of the bundle sheath cells adjacent to the ventral phloem lack chloroplasts.

The lamina arises from the petiole of both species on the ventral side (Fig. 7*C*). However, in the proximal portion of the lamina proper, its bases have dropped from the ventral position to half way down on either side of the midrib, leaving the ventral collenchyma raised into a distinct ventral ridge. This ridge becomes larger up to about half way along the midrib, where it is usually more prominent than the dorsal ridge, although

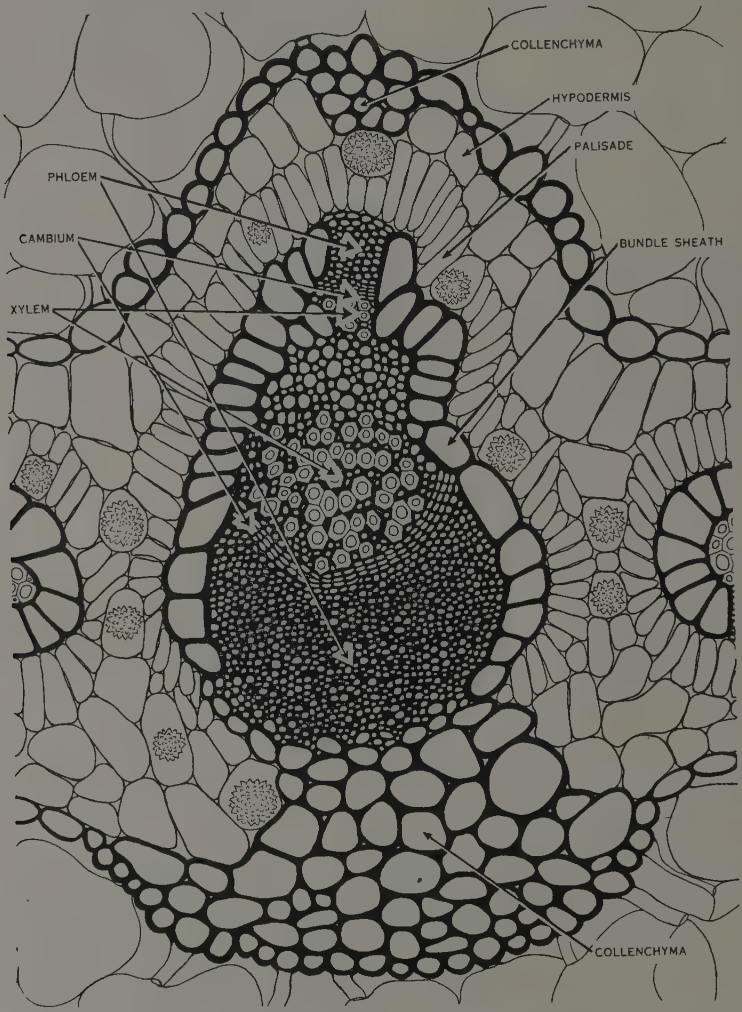


Fig. 8.—Transverse section taken midway along the midrib of a mature leaf of *A. vesicaria.* × 210.

the latter contains more collenchyma. Because of these changes, the large dorsal midrib bundle at this point is usually at the same level as the smaller leaf veins, leaving the ventral bundle more or less contained in the ventral ridge. The ventral ridge of *A. nummularia* half way along the midrib varies from one-third to two-thirds of the mesophyll width, while the dorsal ridge at the same point varies from one-third to one-half the mesophyll width. In *A. vesicaria* the ventral ridge is often larger and up to the full width of the mesophyll in height. From about this point on, in both species, the ventral and dorsal ridges taper away to the leaf tip. Prominent lateral veins (only noticeable in *A. nummularia* specimens) show only a very slight ventral and dorsal swelling with no collenchyma.

Commonly associated with the ventral ridge is a reflexing of the ventral blade surface, at least where the ventral ridge is present. Thus characteristically (most marked in the narrow leaves of *A. vesicaria* specimens) the mature blade has a convex to flat upper surface near the base, with often an acutely concave upper surface near the tip.

The only lignified cell walls in the leaf are those of the actual vessels (shown clear in Figs. 6 and 8). The cambium of the midrib vascular bundles may be inactive (Fig. 8), or active as when thin periclinal division walls can be seen. The phloem elements have extraordinary, thick cellulose (nacré) walls, which are highly hydrated, and dense contents within the commonly very small lumen. Sieve-plates have not been noted from studies of either transverse or longitudinal sections. The degree of cell wall hydration is greatest in the phloem and bundle sheath tissues and least in the collenchyma and epidermal cells of the midrib zone. A similar type of thickening is also a feature of the collenchymatous cells present in and about the xylem of the midrib (Fig. 8).

III. Discussion and Conclusions

Reviewing the angiosperm leaf marginal meristems investigated up to the time, Foster (1936) postulated two distinct types of behaviour of the submarginal initials. In one type anticlinal and periclinal divisions alternate, and the middle layer or layers originate from divisions in various planes of the inner derivatives from the initial cells. In the other type alternating oblique divisions produce two internal layers of cells. At a short and varying distance from the initials, the dorsal internal layer divides periclinally, thus producing a middle layer of cells. Gifford (1951), working with *Drimys,* discovered a third type in which the submarginal initials either divide anticlinally to produce two internal layers, or divide periclinally to produce a middle tier which will then divide to form two internal layers. Subsequently most of the middle layers of the leaf are formed in an indefinite fashion by periclinal divisions of the ventral internal layer. All the leaves examined were dorsoventral with dorsal and middle spongy mesophyll.

It can be seen that the marginal growth of *A. vesicaria* and *A. nummularia* is a combination of the first two types in that they possess a belt of submarginal cells, from the initials to approximately the fourth dorsal cells, which are all capable of dividing periclinally. Thus the two middle layers have separate origins from the submarginal cells. It is open to question at this stage whether this distinction is due to the isobilateral nature of the leaves, or whether it is of taxonomic significance. This question will be answered when the dorsoventral leaves possessed by some species of *Atriplex* have been examined.

It has become generally accepted that the dicotyledonous leaf builds up to its maximum number of layers in thickness close behind the marginal meristem, and that the subsequent growth of the resulting stratified structure is by anticlinal divisions in all of the plate meristems with the exception of those producing the procambia (Avery 1933; Foster 1936; Eames and MacDaniels 1947, p. 321; Esau 1953, p. 445). An exception is the leaf of *Drimys*, where a stratified structure appears to be absent (Gifford 1951). In the *Atriplex* leaves herein examined the occurrence of the ventral hypodermis apparently necessitates the late and regular periclinal division of internal layer 1. The cells cut off to the ventral side immediately vacuolate and enlarge to form the water-storage hypodermis, while the inner layer continues to carry on as a plate meristem for some time and ultimately forms the ventral palisade tissue. These considerations of course do not take into account the great increase in thickness of the mature leaf caused by the profuse production of vesicular hairs from the epidermis.

A vesicular tissue made up of firmly fused vesicles appears to be a characteristic feature of most xerophytic *Atriplex* species. This type of structure was described for *A. farinosa* Forsk. and *A. halimus* L. by Volkens (1884, 1892), and for *A. vesicaria* by Wood (1923). Four distinct functions have been put forward to explain the autecological significance of this tissue. These are:

(1) As a screen to reduce the intensity of excessive illumination (Arcangeli 1890);

(2) As an insulation against excessive transpiration (Wood 1923);

(3) As a water-storage tissue (Volkens 1884, 1892; Wood 1923); and

(4) As a medium to allow the rapid absorption of atmospheric moisture in to the mesophyll of the leaf (Volkens 1884; Wood 1925).

The properties of the tissue necessary for (1) and (2) are self-evident when its structure is considered, particularly under drought conditions when the bulk of the vesicles would be acting as enclosed or partially enclosed air pockets. The potometer experiments carried out in the field by Wood (1923, 1924) clearly illustrate that *A. vesicaria* and tomentose members of the genera *Kochia* and *Rhagodia* have transpiration rates which are lower, and more independent of the external evaporating conditions, than those of mesomorphic and sclerophyllous xeromorphic plants. It follows from (1) and (2) that the vesicular tissue should function as a heat insulator and reflector. The significance of this property is obvious when the intense solar heat and scorching winds, so common under extreme drought conditions, are considered.

In regard to (3) it is true that a relatively large amount of water is stored in the vesicles, particularly in young leaves, but it is difficult to see how this water could be storage in the sense of acting as a reservoir for the replenishment of depleted assimilating cells. In any period of active transpiration there must be an intercellular gradient of vapour pressures which commences at its highest point at the outer surface of the bundle sheath and ends at its lowest point in the external environment outside the vesicular tissue. Furthermore, the vesicles are relatively isolated from the assimilating tissue and separated by the epidermis, and so it can reasonably be expected that the difference between their diffusion pressure deficits would be comparatively large and in a direction causing intracellular water to move outwards from the leaf centre. Thus direct experimental evidence is required before it can be stated that water can move back from the vesicles to the assimilating cells under such conditions. Nevertheless the water contained by the vesicles could still be of indirect value to the assimilating tissue, because by virtue of its presence the vapour pressure gradient could be lengthened, and thus the rate of water flow from the assimilating tissue would be lowered.

In the water-storage hypodermal cells similar considerations apply, with the exceptions that here the tissue is inside the epidermis and in direct contact with the palisade assimilating cells. Thus it is conceivable that, even under the conditions of active transpiration, a transfer of water could take place from the large hypodermal cells back to the much smaller palisade cells, because of the difference between their respective surface/volume ratios.

With regard to (4), the evidence available on the significance of the absorption of atmospheric moisture into the vesicular tissue is conflicting and difficult to assess. There appears to be little doubt that some absorption does take place under conditions of high humidities (greater than 85 per cent., according to Wood 1925), dews, and light rains. However, the natural property of low wettability of the dry vesicle walls forming the outer surface of the leaf tends to minimize the significance of the latter two conditions. This property is most marked in leaves with a very dry surface. On the contrary, with leaves in this condition, the absorption of moisture from external high humidities into the dried outer vesicle walls by imbibitional forces would be at its highest.

It is true that if dead leaves are placed in a high humidity, or in water, for a sufficiently long time, the dead and collapsed vesicles (and other cells) absorb enough water to regain a "turgor", the cell walls and the remains of the cytoplasm apparently acting as a differentially permeable membrane. This process is often utilized in anatomical examinations of dried specimens. In this way, and over an extended period, it would be possible in living but wilting leaves, to reverse the diffusion pressure deficit gradient and thus cause water to move from the outer dead vesicles into the living parts of the leaf. Preliminary experiments designed to test the significance of such a process with *A. vesicaria* (Black 1951) indicated that absorption is too small and too slow to be of importance in considerations of drought resistance. Further work on this problem is being carried out.

Summing up the position from an anatomical point of view, it can be stated that the vesicular tissue in periods of drought possesses properties which mark it as a resistance set in the path of water vapour diffusion from the leaf. As such a resistance it should act both ways. Thus it would appear that the uptake of water from the atmosphere into the living parts of the leaf should be distinctly slower than in a mesomorphic leaf possessing a similar type of epidermis and similar osmotic properties, but lacking a superimposed vesicular structure.

The so-called "Kranz" structure of assimilatory tissue has been reported by Moser (1934) to occur in six genera of the Chenopodiaceae, including *Atriplex, Bassia,* and *Kochia,* as well as in other families of the angiosperms. In an examination of 98 species of *Atriplex* from all parts of the world, he found that the "Kranz" structure occurred in 79 species. The remaining 19 species all had dorsoventral leaves of the normal dicotyledonous type. The author has found the "Kranz" structure to occur in all of the 12 indigenous members of the genus so far examined.

The most striking features of this type of structure are firstly, the fundamental importance of the bundle sheath in the processes of both assimilation and starch storage, and secondly, the remarkably close proximity of all assimilating tissues to the xylem of the leaf vein. It is noticeable, in sections cut of wilting leaves, that a stage can be detected where the thick-walled bundle sheath cells are quite green and healthy, but practically all the outer cells are damaged in one way or another from the effects of water loss. The functional importance of the "Kranz" structure in turgid leaves, as a means of reducing excessive light intensities at the assimilating tissues, was stressed by Arcangeli (1890).

The large area of phloem present in the dorsal midrib vascular bundle (Fig. 8) requires further investigation before it can be separated into its constituent cell types. Their thick, highly hydrated cellulose walls, which are also a feature of other tissues in the leaf, are considered by the author to be worthy of further investigations from a physiological standpoint.

The possible functions of these walls, particularly those of the bundle sheath cells, can be dealt with in two groups. (1) It is becoming widely accepted that the maximum diffusion pressure deficit of a cell is not necessarily limited to its osmotic pressure (Crafts, Currier, and Stocking 1949, p. 75; Kramer 1949, p. 243). This view implies that a state of hydrostatic tension can be set up in the cell, and if this is so, there must be forces capable of firmly retaining the cytoplasm against the cell wall. It is suggested that the cohesive forces of the water phase, common to the highly hydrated cell wall and the peripheral cytoplasm, would fill these requirements. The thickened wall should also help to prevent the entry of air into the cell and crumpling of the cell wall during desiccation.

(2) The walls, by virtue of their thickness and hydration, should control very effectively by imbibitional forces the rate of water loss from the cells relative to the external vapour pressure. This is the process of incipient drying as put forward by Livingston and Brown (1912).

A feature of the midrib of both *A. vesicaria* and *A. nummularia* is its pronounced ventral development, and the presence over the greater part of the length of the lamina of a distinct ventral vascular bundle. This ventral ridge is present (though to a lesser degree) in a few other indigenous species, and conspicuously absent from another large group. Thus it is suggested that this feature, together with its apparently associated effect of reflexing the ventral blade surface, may be of some use in the taxonomy of the genus.

IV. ACKNOWLEDGMENTS

Thanks are due to Dr. N. C. W. Beadle, University of Sydney, for the original suggestion on the need for the present work, and for assistance throughout its production. The author is also greatly indebted to a number of the staff members from the Botany Department and Plant Physiology Unit, C.S.I.R.O., University of Sydney, for a great deal of assistance and helpful criticism during all phases of the work.

V. REFERENCES

AELLEN, P. (1938).—Revision der australischen und neuseeländischen Chenopodiaceen. I. *Sonderdr. Bot. Jb.* 68: 345-434.

ANDERSON, R. H. (1930).—Notes on the Australian species of the genus *Atriplex*. *Proc. Linn. Soc. N.S.W.* 55: 493-505.

ARCANGELI, G. (1890).—Sulla struttura delle foglie dell *Atriplex nummularia* Lind. in relazione alla assimilazione. *Nuovo G. Bot. Ital.* 22: 426-30.

AVERY, G. S. (1933).—Structure and development of the tobacco leaf. *Amer. J. Bot.* 20: 565-92.

BLACK, J. M. (1948).—"Flora of South Australia." Part II. 2nd Ed. (Govt. Printer: Adelaide.)

BLACK, R. F. (1951).—The halophilous and xerophytic properties of the genus *Atriplex*. Honours Thesis, University of Sydney.

CRAFTS, A. S., CURRIER, H. B., and STOCKING, C. R. (1949).—"Water in the Physiology of Plants". p. 75. (Chronica Botanica Co.: Waltham, U.S.A.)

EAMES, A. J., and MACDANIELS, L. H. (1947).—"An Introduction to Plant Anatomy". 2nd. Ed. p. 321. (McGraw-Hill Book Co.: New York.)

ESAU, K. (1953).—"Plant Anatomy". p. 445. (John Wiley & Sons: New York.)

FOSTER, A. S. 1936).—Leaf differentiation in angiosperms. *Bot. Rev.* 2: 349-72.

GIFFORD, E. M. (1951).—Early ontogeny of the foliage leaf in *Drimys winteri* var. *chilensis*. *Amer. J. Bot.* 38: 93-104.

KRAMER, P. J. (1949).—"Plant and Soil Water Relationships". 1st Ed. p. 243. (McGraw-Hill Book Co.: New York.)

LIVINGSTON, B. E., and BROWN, W. H. (1912).—Relation of the daily march of transpiration to variations in the water content of foliage leaves. *Bot. Gaz.* 53: 309-30.

MOSER, H. (1934).—Untersuchungen über die Blattstruktur von *Atriplex* — Arten und ihre Beziehungen zur Systematik. *Beih. bot. Zbl.* 52: 378-88.

VOLKENS, G. (1884).—Zur Kenntniss der Beziehungen zwischen Standort und anatomischem Bau der Vegetationsorgane. *Jb. Berl. Bot. Gart.* 3: 37 et seq.

VOLKENS, G. (1892).—Chenopodiaceae *in* "Die natürlichen Pflanzenfamilien." III. Teil 1. Abteilung *a*: 36-91.

WINKLER, H. (1939).—Versuch eines "natürlichen" Systems der Früchte. *Beitr. Biol. Pfl.* 26: 201-20.

WOOD, J. G. (1923).—Transpiration of some plants from the arid portions of South Australia, with notes on their physiological anatomy. *Trans. Roy. Soc. S. Aust.* 47: 259-78.

WOOD, J. G. (1924).—Relations between distribution, structure, and transpiration of arid South Australian plants. *Trans. Roy. Soc. S. Aust.* 48: 226-35.

WOOD, J. G. (1925).—Selective absorption of chlorine ions, and absorption of water by the leaves in the genus *Atriplex*. *Aust. J. Exp. Biol. Med. Sci.* 2: 45-56.

EXPLANATION OF PLATES 1-3

PLATE 1

Transverse sections of primordial laminae of *A. nummularia*. All × 850.

Fig. 1.—Showing the separate origins of internal layers 2 and 3 by periclinal divisions (*P.D.*) of the submarginal initial and a dorsal derivative. Section also shows two divisions in internal layer 2, parallel to the plane of lamina. *V.I.B.*, an early stage of a vesicle initial "blowout."

Fig. 2.—Showing an anaphase figure of division parallel to the plane of the lamina in internal layer 2.

Fig. 3.—Marginal development as in Figure 1, and in addition two periclinal divisions in internal layer 4 near the midrib.

PLATE 2

Figs. 1 and 2.—Four developmental stages of the vesicular hair of *A. nummularia*, as seen in transverse sections of a primordial lamina. 1, metaphase figure in a dermatogen cell producing a vesicle initial; 2, a vesicle initial completely formed; 3, metaphase figure of the division of an initial which produces a stalk cell; 4, a young vesicular hair complete with one stalk cell. × 2000.

Fig. 3.—Surface view of a young *A. vesicaria* leaf, showing the fused and stretched walls of four collapsing vesicles, with an air bubble (*A.B.*) in one of them. × 145.

Fig. 4.—As above, but showing one fused vesicle being stretched in three directions. × 145.

PLATE 3

Figs. 1-3.—Surface views of field specimens of *A. vesicaria* leaves.

Fig. 1.—Ventral surface of a young leaf, 4 mm long, and from the bud. Vesicles are turgid right to the surface. × 145.

Fig. 2.—Slightly older leaf, 6 mm long, and free from the bud, showing the development of a surface film of partially collapsed vesicles. × 145.

Fig. 3.—Old leaf with typical segmented vesicular layer. Turgid vesicles can be seen between the segments. × 55.

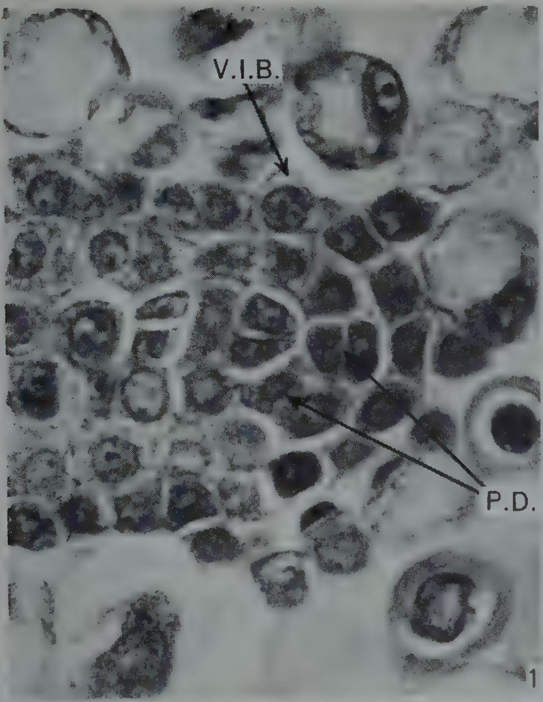
Figs. 4-6.—Surface views of *A. nummularia* leaves from plants grown in Sydney under glass.

Fig. 4.—Young leaf free from bud; leaf blade 10 mm long. × 55.

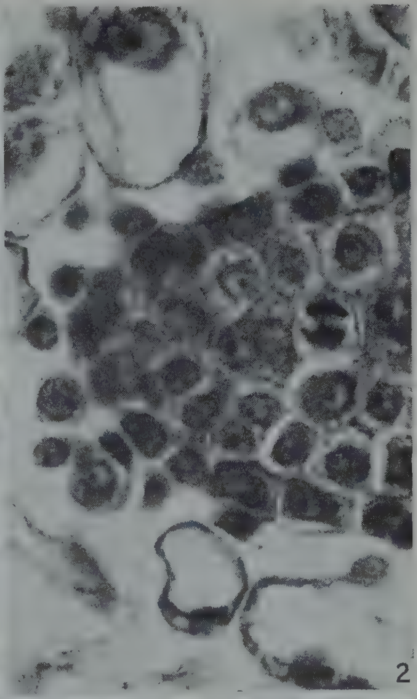
Fig. 5.—Same leaf as above. Note the ovoidal shape of the mature vesicle. × 145.

Fig. 6.—Mature leaf, leaf blade 20 mm long. Shows a surface film of probably a single layer of dead, fused, and completely collapsed vesicles. Turgid vesicles are visible in places. × 145.

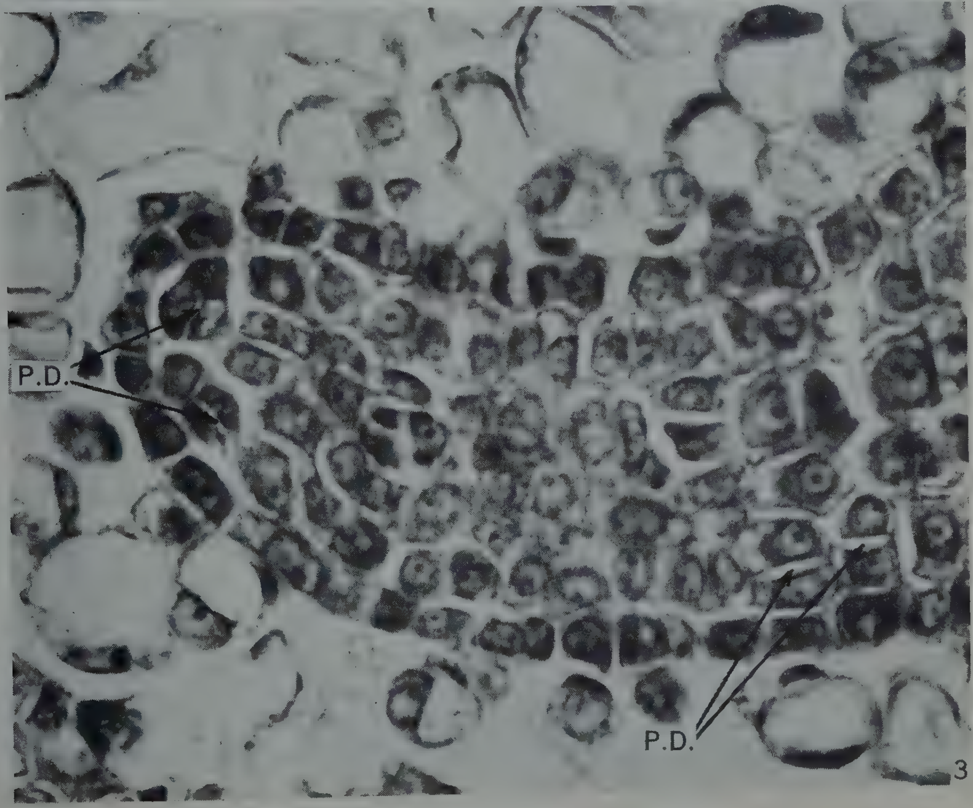
LEAF ANATOMY OF AUSTRALIAN ATRIPLEX. I



1



2



3

CHROMOSOME NUMBERS IN THE BORONIEAE (RUTACEAE) AND THEIR BEARING ON THE EVOLUTIONARY DEVELOPMENT OF THE TRIBE IN THE AUSTRALIAN FLORA

By S. Smith-White*

(*Manuscript received April* 8, 1954)

Summary

Chromosome numbers are reported for 69 species, belonging to 11 genera of the Boronieae. In comparison with the other divisions of the Rutaceae, chromosome numbers are remarkably variable, and base numbers range from 7 to 19. Seven genera and 10 species belonging to other tribes and subfamilies of the Rutaceae are also reported.

In common with the Aurantoideae, Xanthoxyleae, and Ruteae, the primitive number in the Boronieae is almost certainly 9. Chromosomal evolution has involved both aneuploidy and polyploidy.

In both diploid and polyploid species, chromosome pairing is essentially regular. All the polyploids, even within recognized taxonomic species, are essentially of allopolyploid constitution.

Two stages in the occurrence of polyploidy can be recognized — the first giving rise to groups of generic status, and the second to polyploid species within genera.

Many genera possess chromosome numbers which could be derived by aneuploid reduction, followed by polyploidy.

Some fundamental change in chromosome structure in the primitive Boronieae stock is suggested as a cause of its early chromosomal instability.

From a correlation of geographical and cytological data and inference, a hypothesis of the historical development of the Boronieae in Australia is presented. Following their isolation in the continent, and the occurrence of a fundamental reorganization in chromosome structure, a period of generic radiation, with changes in basic number, occurred before the Miocene.

Particular chromosome numbers are characteristic of genera. Differences in base number rank as generic rather than as specific criteria. On this basis the accepted taxonomy is essentially sound, and only minor alterations are suggested. *Crowea* is established, and *Eriostemon lanceolatus* is separated from its congeners. Some sections of *Boronia* are deserving of generic rank, and *B. serrulata* is wrongly placed in the section *Terminales*.

I. Introduction

The tribe Boronieae constitutes one of several tribes of the subfamily Rutoideae of the Rutaceae. It is predominantly Australian, but several small endemic genera occur in New Caledonia. The tribe can be regarded as part of the autochthonian or paleoaustralian element in the Australian flora. Diels (1936) has suggested that it represents a specialized development of the paleotropical Xanthoxyleae, and that it demonstrates a relationship between the older floras of Australia and south-east Asia.

* Botany Department, University of Sydney.

Other tribes of the Rutoideae, and other subfamilies of the Rutaceae, occur in Australia, but, with the exception of one species of *Geijera,* are restricted to north-eastern regions of the continent, in tropical and subtropical rain-forest areas. The marked endemism of the Boronieae is not found in these other groups, where endemism scarcely exceeds the specific level. The Xanthoxyleae, Toddalioideae, and Aurantoideae in Australia are Malesian rather than paleoaustralian in character. The Flindersioideae, considered by Engler to be a subfamily of the Rutaceae, but placed in the Meliaceae by Bentham, are chiefly Australian, but their restriction to eastern and northern Australia and almost complete limitation to rain-forest conditions, also suggest their Malesian and neoaustralian nature.

The Boronieae have a distribution extending over the whole of the Australian continent, and they show the high degree of xeromorphic adaptation characteristic of other paleoaustralian groups. They also show a clear and sharp division, within the continent, into two regions of specific endemism—a larger eastern area, and a smaller western one. Very few species, possibly none, are common to both of these regions. Bentham (1863) listed six species, of the 143 then recognized, as being represented in both regions, but the identifications are doubtful in some cases, while in others the species are represented by distinct varieties in the east and west, and some of these varieties have since been raised to specific rank. All the species which have been described since 1863, of which there are about 100, are of restricted distribution, and none are common to both regions. Even with respect to genera, there is a marked differentation of the two subcontinental regions. Of the 16 recognized Australian genera, two are endemic to the east, and seven to the west. Only seven genera are common to both regions, but in the large genus *Boronia,* several sections, which may deserve generic rank, are also restricted to the west. Acceptance of a paleoaustralian development of the tribe seems entirely justified.

Records of chromosome numbers in the Rutaceae

Known chromosome numbers in the Rutaceae are listed in Table 1, which has been compiled chiefly from Darlington and Janaki (1944). Outside the Aurantoideae, the data are scanty.

Except for a few triploid and tetraploid species and horticultural varieties in *Citrus,* which are either apomictic, or probably apomictic, and for high polyploids in *Xanthoxylum* and *Ruta,* there is little deviation from the haploid number 9. Such deviations as do occur involve only polyploidy. Darlington (in Darlington and Janaki 1944) commented upon this uniformity in chromosome number in the family, and there can be little doubt that the basic chromosome set for the family was, and is, 9. This view is supported by the occurrence of polyploid numbers on base 9 in the related families Simarubaceae (*Quassia amara,* $2n = 36$) and the

Meliaceae (*Dysoxylum ramiflorum*, $2n = 72$) and in the Flindersioideae (*Flindersia* spp. $2n = 36$, 108, cf. Table 3).

TABLE 1

RECORDED CHROMOSOME NUMBERS IN THE RUTACEAE

Group and Species	Chromosome Number ($2n$)	Authority
Rutoideae		
Ruteae		
Ruta palavina	18 ($2x$)	Capelletti 1929
R. graveolens	81 ($9x$)	Revel*
Dictamnus albus	36 ($4x$)	Bowden 1945
Evodia fraxinifolia	72 ($8x$)	Bowden 1945
E. hupehensis	72 ($8x$)	Bowden 1945
E. danielli	72 ($8x$)	Bowden 1945
Bonninghausenia albiflora	18 ($2x$)	Sugiura 1936
Xanthoxyleae		
Xanthoxylum clava-herculis	72 ($8x$)	Bowden 1940
X. piperitum	70	Nakajima 1937
X. americana	68	Walker 1942
Aurantoideae		
Aegilopsis chevaliere	18 ($2x$)	Longley 1925
Afraegle gabonensis	18 ($2x$)	Krug 1943
Atalantia citrioides	18 ($2x$)	Krug 1943
Clausenia lansium	18 ($2x$)	Krug 1943
Feronia limonia	18 ($2x$)	Toxopeus 1933
Murraya koenigii	18 ($2x$)	Janaki 1944
M. paniculata	18 ($2x$)	Toxopeus 1933
Microcitrus australasica	18 ($2x$)	Grug 1943
Citrus spp. (30 spp.)	18 ($2x$)	Cf. Darlington and Janaki 1944
(5 spp. and vars.)	27 ($3x$)	
(10 spp. and vars.)	36 ($4x$)	
(1 var.)	45 ($5x$)	
Triphasia triflora	18 ($2x$)	Longley 1925
T. triflora	36 ($4x$)	Krug 1943
Fortunella crassifolia	18 ($2x$)	Longley 1925
F. japonica	18 ($2x$)	Longley 1925
F. margarita	18 ($2x$)	Lapin 1937
F. lindsii	18 ($2x$)	Longley 1925
	36 ($4x$)	Longley 1925
Poncirus trifoliata	18 ($2x$)	Longley 1925
	18, 36 ($2x$, $4x$)	Lapin 1937
Aegle marmelos	36 ($4x$)	Janaki 1944

* For references (other than Bowden 1945) see Darlington and Janaki (1944).

Whilst polyploidy has been of some importance in the evolutionary development of the Rutaceae, aneuploid changes have not occurred at all. Darlington has suggested that this absence of aneuploid change may imply a type of chromosome organization which reduces or inhibits the occurrence or survival of translocations and interchange.

II. Materials and Methods

The present cytological survey of the Boronieae covers 11 genera and approximately 70 species. Although the tribe includes 16 genera and over 200 species in Australia, the species examined may be reasonably accepted as representative, and competent to give a reliable picture of cytological conditions in the tribe.

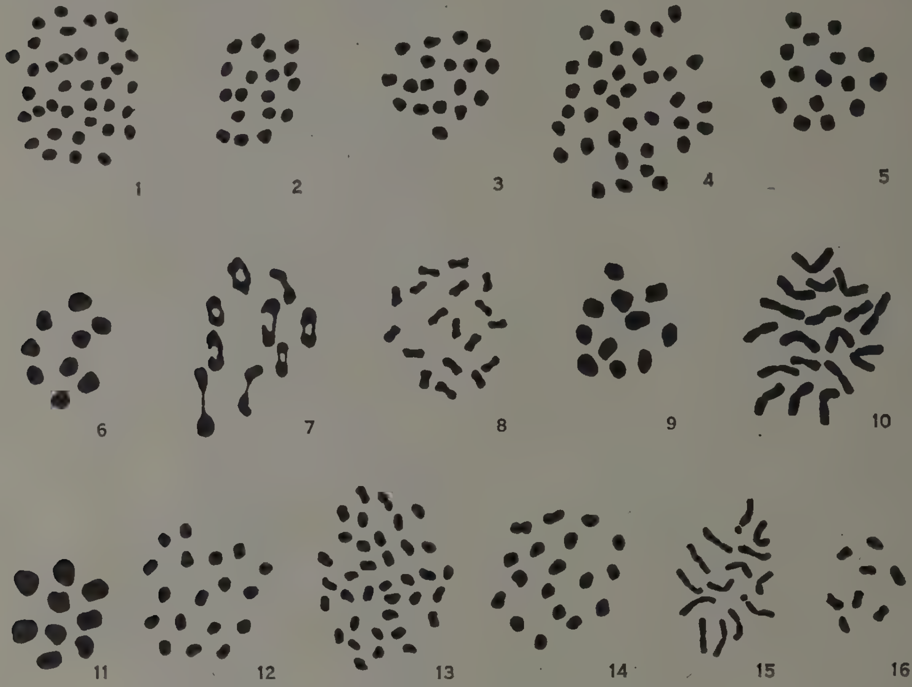


Fig. 1.—*Zieria laevigata,* Kuringai, *M*1. Fig. 2.—*Z. laevigata,* Evans Head, *M*1. Fig. 3.—*Z. pilosa, M*1. Fig. 4.—*Z. smithii,* Newport, *M*1. Fig. 5.—*Boronia triphylla, M*1. Fig. 6.—*B. nematophylla, M*1. Fig. 7.—*B. nematophylla, A*1. Fig. 8.—*B. crenulata, M*2, one plate only. Fig. 9.—*B. serrulata, M*1. Fig. 10.—*B. barkeriana,* somatic metaphase (leaf initial). Fig. 11.—*B. barkeriana, M*1. Fig. 12.—*B. coerulescens,* Kangaroo I. *M*1. Fig. 13.—*B. coerulescens,* Port Lincoln, *M*1. Fig. 14.—*B. anemonifolia, M*1. Fig. 15.—*B. pulchella,* somatic metaphase (leaf initial). Fig. 16.—*B. gracilipes, M*2, one plate only. All × 2600.

Where possible, wild growing plants have been preferred for study. For some species, only cultivated plants were available. Counts have been made chiefly from meiotic stages in pollen mother cells, but in a few species determinations have been made from mitotic metaphases in leaf bud and young ovary tissue. Aceto-orcein, aceto-lacmoid, and Feulgen crush techniques have been employed.

III. Observations

A summary of the material studied, and of the chromosome number determinations made, is given in Tables 2 and 3.

TABLE 2
CHROMOSOME NUMBERS IN THE BORONIEAE

Genus and Species	State	Localities	Chromosome Number		Reference
			n	$2n$	
Subtribe Boroninae					
Zieria Sm. $x = 18$					
Zieria laevigata Sm.	N.S.W.	Kuringai, Warrah La Perouse, Rylstone	36	—	Figure 1
Z. laevigata (?)	N.S.W.	Evans Head	18	—	Figure 2
Z. aspalathoides A. Cunn.	N.S.W.	Rylstone	36	—	
Z. pilosa Rudge	N.S.W.	Kuringai, Warrah	18	—	Figure 3
Z. cytisoides Sm.	N.S.W.	Rylstone	36	—	
Z. smithii Andr.	N.S.W.	Heathcote	18	—	
Z. smithii Andr.	N.S.W.	Newport, Kuringai	36	—	Figure 4
Boronia Sm. $x = 9, 8, 7, 11, 16$					
Section I Valvatae. $x = 16$					
B. ledifolia Gay	N.S.W.	Kuringai, Berowra	16	—	
B. ledifolia var.	N.S.W.	Copmanhurst	16	—	
B. triphylla Sieb.	N.S.W.	National Park	16	—	Figure 5
B. fraseri Hook.	N.S.W.	Berowra	16	—	
B. mollis A. Cunn.	N.S.W.	Warrah	16	—	
Section II Imbricatae					
Subsection Terminales. $x = 9, 11$					
B. nematophylla F. Muell.	W.A.	Cranbrook	9	—	Figures 6, 7
B. crenulata Sm.	W.A.	Manjimup, Chester Pass	18	—	Figure 8
B. serrulata Sm.	N.S.W.	Nat. Park, Kuringai	11	22	Figure 9
B. parviflora Sm.	N.S.W.	Kuringai, Warrah	9	18	
B. barkeriana F. Muell.	N.S.W.	Blackheath, Carrington	9	18	Figures 10, 11
B. viminea Lindl.	W.A.	Cannington, Bull's Creek	9	—	
Subsection Pedunculatae. $x = 9$					
B. fastigata Bartl.	W.A.	Gleneagle	9	—	
B. spathulata Lindl.	W.A.	Porongorups	9	—	
B. denticulata Sm.	W.A.	Lower Kalgan R.	9	—	
Subsection Cyaneae. $x = 9$					
B. coerulescens F. Muell.	S.A.	Kangaroo I.	18	—	Figure 12
B. coerulescens F. Muell.	S.A.	Pt. Lincoln	36	—	Figure 13
B. tenuis Benth.	W.A.	Albany	9	—	
B. ramosa Benth.	W.A.	Gnangara	18	—	
Subsection Variabiles. $x = 18$					
B. polygalifolia Sm.	N.S.W.	Concord	18	—	
B. anemonifolia A. Cunn.	N.S.W.	Blackheath, Rylstone	18	—	Figure 14
B. rigens Cheel	N.S.W.	Kuringai	18	—	

TABLE 2 (*Continued*)

Genus and Species	State	Localities	Chromosome Number		Reference
			n	$2n$	
Subsection Pinnatae. $x = 7, 8, 11$					
B. pulchella Turcz.	W.A.		—	14	Figure 15
B. gracilipes	W.A.	Nornalup	8	—	Figure 16
B. microphylla Sieb.	N.S.W.	Rylstone, Blackheath	11	22	Figure 17
B. pinnata Sm.	N.S.W.	Kuringai	11	22	Figures 18, 19
B. floribunda Sieb.	N.S.W.	National Park	11	22	Figure 20
B. thujona Cheel.	N.S.W.	National Park	11	22	
B. pilosa Labill.	N.S.W.	Eden	11	—	
Section III Heterandreae. $x = 9, 8, 7$					
B. megastigma Nees	W.A.	Manjimup. Also cult.	7	14	Figures 21, 22
B. heterophylla F. Muell.	W.A.	Cult.			
B. elatior Bartl.	W.A.	Albany	—	16	Figures 23, 24
B. purdiana Diels	W.A.	Gnangara	9	18	Figure 25
B. crassifolia Bartl.	W.A.	Warrengup, Stirling Ra.	9	—	Figures 26, 27
B. crassifolia Bartl.	W.A.	Warrengup, Stirling Ra.	18	—	Figures 28, 29
Subtribe Eriostemoninae					
Eriostemon Sm. $x = 14, 17$					
E. lanceolatus Gaertn.	N.S.W.	Kuringai, Warrah	17	—	Figure 30
E. myoporoides DC	N.S.W.	Nepean R. Also cult.	14	—	Figure 32
E. hispidules Sieb.	N.S.W.	Springwood	14	—	
E. buxifolius Sm.	N.S.W.	National Park, Kuringai	14	—	
E. obovalis A. Cunn.	N.S.W.	Blackheath	14	—	
E. scaber Paxt.	N.S.W.	Liverpool	14	—	
E. spicatus A. Rich.	W.A.	King's Park	28	—	Figure 31
E. brevifolius A. Cunn.	S.A.	Mt. Lofty	28	—	Figures 33, 34
Crowea Sm. $x = 19$					
C. saligna Andr.	N.S.W.	Kuringai, Berowra	19	—	Figure 35
C. dentata R.Br.	W.A.	Manjimup, Pemberton	19	—	Figure 36
Phebalium A. Juss. $x = 16$					
Section Leionema					
P. dentatum Sm.	N.S.W.	Lane Cove R., Warrah	16	—	Figure 37
P. ralstoni Benth. var.	N.S.W.	Rylstone	16	—	
P. diosmeum A. Juss.	N.S.W.	Heathcote	16	—	
Section Euphebalium					
P. ozothamnoides F. Muell.	N.S.W.	Mt. York	32	—	Figure 38
P. glandulosum Vent.	N.S.W.	Cult. Dripstone	16	—	
P. squamulosum Vent.	N.S.W.	Kuringai, Blackheath	16	—	

TABLE 2 (*Continued*)

Genus and Species	State	Localities	Chromosome Number		Reference
			n	$2n$	
P. squameus Labill.	Tas.	National Park	16	—	
P. billardieri A. Juss.	N.S.W.	Springwood	16	—	
P. drummondii Benth.	W.A.	Morowa	32	—	
P. microphyllum Turcz.	W.A.	Morowa	32	—	
P. sp. SA52/21	S.A.	Pt. Lincoln	16	—	
Geleznowia					
G. verrucosa Turcz.	W.A.	Coorow	14	—	Figure 39
Asterolasia F. Muell. $x = 13, 14$					
Section Euasterolasia					
A. correifolius Benth.	N.S.W.	Berowra	14	—	Figure 41
Section Urocarpus					
A. dielsii Gardner	W.A.	Gleneagle	13	—	Figure 42
Philotheca Rudge. $x = 14$					
Section Euphilotheae					
P. australis Rudge	N.S.W.	Kuringai	14	—	
P. reichenbachiana Sieb.	N.S.W.	Lane Cove R.	14	—	
Section Drummondita					
P. miniata Gardner	W.A.	Mullewa, Coorow	14	—	Figure 40
Subtribe Correinae					
Correa Sm. $x = 16$					
C. alba Andr.	N.S.W.	Austinmer, Maroubra	16	—	Figure 43
C. speciosa Ait.	N.S.W.	Lane Cove R., Audley	16	—	
C. lawrenciana Hook.	N.S.W.	Milton. Clyde R.	16	—	
Subtribe Nematolepidinae					
Chorilaena. $x = 14$					
C. quercifolia Endl.	W.A.	Nornalup	14	—	Figure 44
C. hirsuta Benth.	W.A.	Nannup	14	—	
Subtribe Diplolaeninae. $x = 13?$					
Diplolaena. $x = 13?$					
D. grandiflora Desf. (?)	W.A.	Nedlands (cult.)	13	—	Figure 45

All the species examined appear normally to be fully pollen fertile, with reasonably regular meiosis and normal tetrad production. However, meiotic irregularities were found occasionally in almost all plants of all species examined. Chromosome bridges were seen in most species, their frequency usually being below 1 per cent., but occasionally as high as 5 per cent. of the pollen mother cells in first or second anaphase. This higher frequency was approached in one plant of *Eriostemon lanceolatus*, and in the only plant of *E. brevifolius* examined. In one plant of *E.*

obovalis, all the mother cells seen at first anaphase had bridges, with often as many as three in the one cell. It was not usually possible to determine whether bridges were of the "sticky" or subchromatid type, or whether they were true inversion bridges. In a few examples, fragments could be identified (Fig. 19), and inversion hybridity can be inferred. Bridges often result in chromatin connections between telophasic nuclei, and in the exclusion of chromatin from the reconstituted nuclei (Fig. 20). If many of the bridges seen are of the inversion type, outbreeding systems would be indicated as characteristic of the tribe. Nondisjunction, or late disjunction, univalents, and laggards at *A*1 were seen occasionally, and in some (Fig. 34) misdivision of univalents is suggested.

TABLE 3

ADDITIONAL CHROMOSOME NUMBERS IN THE RUTACEAE, EXCEPTING THE BORONIEAE

Genus and Species	State	Localities	Chromosome Number		Reference
			n	2*n*	
Subfamily Rutoideae					
Tribe Xanthoxyleae.					
$x = 9$?					
Geijera parviflora Lindl.	N.S.W.	Botanic Gardens (cult.)	54	108	Figure 47
Evodia micrococca F. Muell.	N.S.W.	Ourimbah	—	36	Figure 46
Tribe Diosmeae. $x = 9$?					
Calodendron capense L.f.	S. Africa	Sydney (cult.)	27	54	Figures 49, 50
Coleonema pulchrum Hook.	S. Africa	Sydney (cult.)	—	36	Figure 48
Subfamily Toddalioideae.					
$x = 9$?					
Acronychia laevis Forst.	N.S.W.	Ourimbah	—	36	Figure 53
Subfamily Flindersioideae.					
$x = 9$?					
*Flindersia** *australis* R.Br.	Qld.		—	108	Figure 52
F. bourjotiana F. Muell.	Qld.		—	36	
F. oxleyana F. Muell.	Qld.		—	36	
F. pubescens F. Muell.	Qld.		—	36	Figure 51
F. schottiana F. Muell.	Qld.		—	36	

* Material of *Flindersia* examined was obtained from germinating seed. Seed supplied Brisbane.

Throughout the group, the species show no extreme variations in chromosome size. The largest are those of *Asterolasia correifolius* (Fig. 41), whilst the smallest belong to polyploid species in *Eriostemon*, *Phebalium*, and *Zieria*. In general, where a polyploid series exists within a genus, the chromosomes of the polyploids are reduced in size as compared with the diploids (compare Figs. 26 and 28). This comparison suggests that such polyploids have been subject to selection for optimum cell and chromosome size. The fertility of the polyploids, the wide geographical ranges of many, and the low frequency of multivalents, indicate their status as well-established allopolyploids.

There are few examples of intraspecific polyploidy. In *Zieria smithii, Z. laevigata,* and *Boronia coerulescens* the polyploids came from widely separated localities, and all three species exist in several "varietal" forms. In *Boronia crenulata,* intraspecific polyploidy is reported for plants from different localities, but the species appears to be morphologically uniform. In *Boronia crassifolia* (Figs. 26, 27, 28, 29) diploids and tetraploids were found together in the same community, on a steep mountainside at Warrengup, W.A. In both diploid and tetraploid forms, meiosis is normal, with regular bivalent formation and an absence of multivalents. From the superficial examination possible at the time, it appeared that the diploid and polyploid forms differed mainly in the number and size of the flower

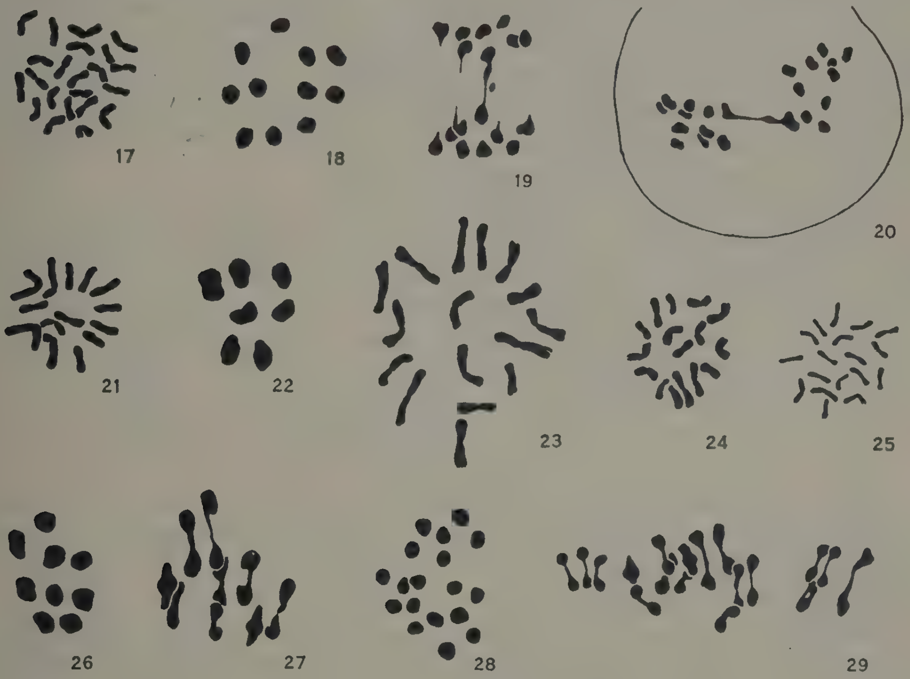


Fig. 17.—*Boronia microphylla.* Somatic metaphase (leaf initial). Fig. 18.—*B. pinnata, M*1. Fig. 19.—*B. pinnata, A*1, with bridge and fragment. Fig. 20.—*B. floribunda, M*2, with a residual bridge. Fig. 21.—*B. megastigma,* somatic metaphase (leaf initial). Fig. 22.—*B. megastigma, M*1. Figs. 23, 24.—*B. elatior.* Two somatic metaphases from the same leaf initial, showing extreme differences in chromosome size. Fig. 25.—*B. purdiana.* Somatic metaphase (leaf initial). Figs. 26-29.—*B. crassifolia.* Fig. 26.—*M*1, diploid form. Fig. 27.—Early *A*1, diploid form. Fig. 28.—*M*1, tetraploid form. Fig. 29.—Early *A*1, tetraploid form. Chromosome pairing is quite regular. All × 2600.

buds. If this difference should prove characteristic, then the diploids are more frequent at the foot of the mountain, and the polyploids are most numerous at or near the summit.

In most or all species, all chromosomes of the complement are of similar size, and in few are there any obvious differences in chromosome morphology. In *Asterolasia correifolius* (Fig. 41) there is a bivalent which has a distinct satellite. In species examined in mitotic metaphase, the chromosomes are short rods, 1.5-2.5 μ in length, with submedian to subterminal centromeres. To have any significance, chromosome length measurements would need to be replicated, since in different cells of the same leaf-bud crush considerable variation occurs (Figs. 23, 24). Such measurements should be made on sectioned material, where the actual tissue can be identified, rather than on crushes.

The most interesting series in comparative chromosome morphology is to be found in the section *Heterandreae* of *Boronia*, where haploid numbers of 9, 8, and 7 occur. In *B. megastigma* ($n = 7$, Fig. 21) two pairs of chromosomes are distinctly longer than the others at mitotic metaphase, and can be recognized as sharply bent rods, with median centromeres. It is likely that this difference in form and reduction in number within the complement are the result of interchange and centromere loss.

IV. Discussion

Cytological conditions in the Boronieae have significance for the taxonomic subdivision of the tribe, and they have an important bearing on the interpretation of the phylogeny and the historical development of the group in Australia.

The use of chromosome numbers in the taxonomic subdivision of any group may lead to serious error unless correlated with evidence derived from other disciplines. Smith (1933) has shown that in *Primula* a purely chromosomal classification yields an artificial result. In *Crepis* there have been parallel trends in chromosomal evolution in different sections of the genus (Babcock 1947), and in *Calochortus* increase in chromosome number has occurred independently in the three sections (Beal and Ownby 1943). Nevertheless, differences in chromosome number and morphology are likely to reflect the evolutionary processes which have contributed to the development of a group. If phyletic relationship is accepted as a basis of taxonomy, cytological conditions must have a significance exceeding that of ordinary morphological characters.

(*a*) *Chromosome Evolution*

There can be little doubt that the primitive basic number in the Boronieae, in common with the other subfamilies and tribes of the Rutaceae, is 9, since this number is still found in several sections of *Boronia*. Modification of this primitive chromosome set has apparently involved two kinds of change — a stepwise decrease or increase in base number, and polyploidy — so that almost every number from 7 to 19 is now represented. This condition of instability is in striking contrast to the stability and uniformity of chromosome number in the Aurantoideae, which has been commented upon by Darlington (Darlington and Janaki 1944). The possible relationships and derivations of the different numbers in the Boronieae are illustrated in Figure 54. The diagram is not intended to represent phyletic relationships between genera, since similar chromosome numbers have almost certainly been derived independently.

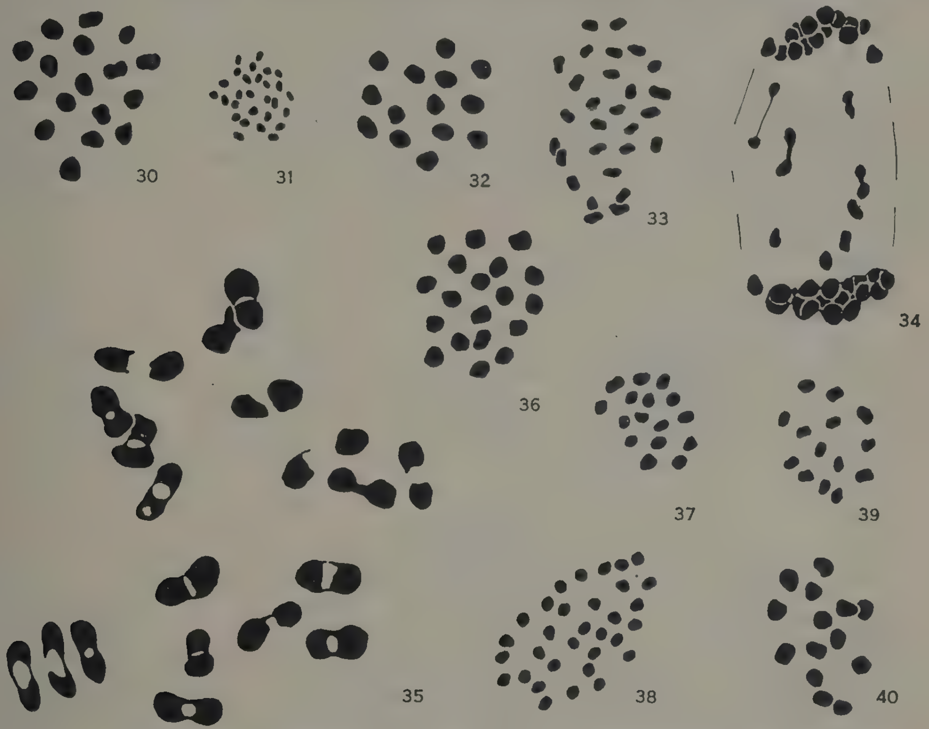


Fig. 30.—*Eriostemon lanceolatus, M*1. Fig. 31.—*E. spicatum, M*2, one plate only. Fig. 32.—*E. myoporoides, M*1. Fig. 33.—*E. brevifolius, M*2, one plate only. Fig. 34.—*E. brevifolius, A*1, with numerous laggards and univalents, some showing misdivision. Fig. 35.—*Crowea saligna, M*1 or early *A*1, squashed. Fig. 36.—*C. dentata, M*1. Fig. 37.—*Phebalium dentatum, M*1. Fig. 38.—*Ph. ozothamnoides, M*1. Fig. 39.—*Geleznowia verrucosa, M*1. Fig. 40.—*Philotheca miniata, M*1. All × 2600.

The mechanisms by which change in basic number may occur were first suggested by Darlington (1937), and have since been verified by Tobgy (1943), Sherman (1946), and Hakansson (1946). Darlington (Darlington and Janaki 1944) suggested that a liability to the establishment of such changes, either upwards or downwards, may depend on the organization of heterochromatin with respect to the centromeres. In the mitotic karyotype of *Boronia megastigma* ($n = 7$) the presence of two pairs of long chromosomes suggests the past occurrence of translocation or interchange of the type demonstrated by Tobgy (1943) in *Crepis.*

The other source of chromosomal change in the Boronieae has been by allopolyploidy. Changes in ploidy have occurred on numerous occasions, but two stages may be recognized; an older, involving genera or sections of a genus, and a younger, involving species within a genus.

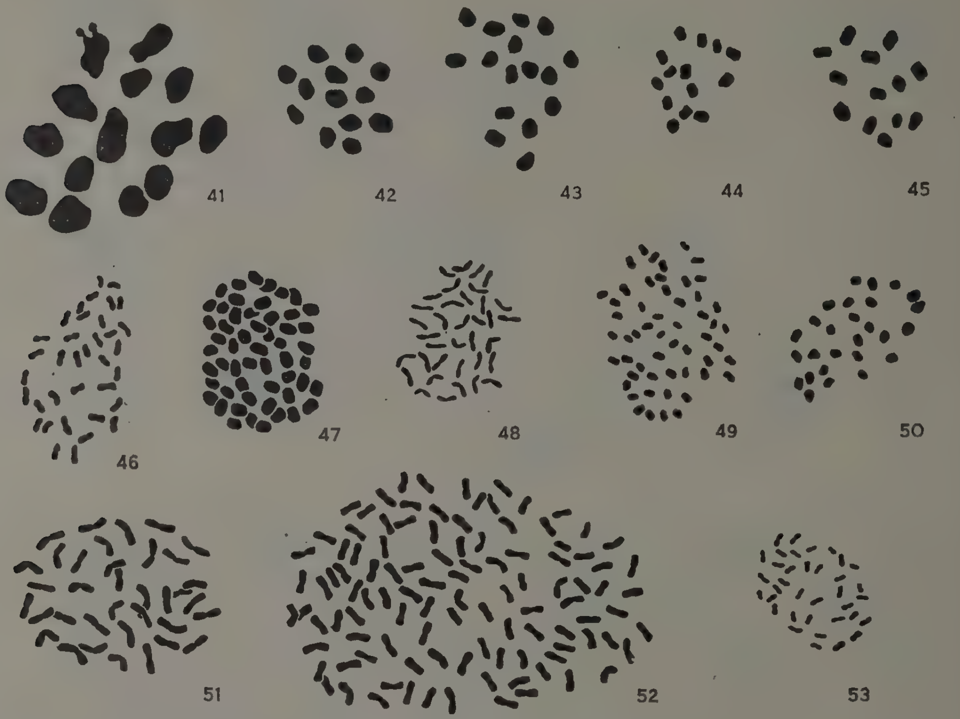


Fig. 41.—*Asterolasia correifolius, M*1. Fig. 42.—*A. deilsii, M*1. Fig. 43.—*Correa alba, M*1. Fig. 44.—*Chorilaena quercifolia, M*2, one plate only. Fig. 45.—*Diplolaena grandiflora, M*2, one plate only. Fig. 46.—*Evodia micrococca.* Somatic metaphase (leaf initial). Fig. 47.—*Geijera parviflora, M*2, one plate only. Fig. 48.–-*Coleonema pulchra,* somatic metaphase (leaf initial). Fig. 49.—*Calodendron capense.* Somatic metaphase (leaf initial). Fig. 50.—*C. capense, M*2, one plate only. Fig. 51.—*Flindersia pubescens.* Somatic metaphase (root tip). Fig. 52.—*F. australis.* Somatic metaphase (root tip). Fig. 53.—*Acronychia laevis.* Somatic metaphase (leaf initial). All × 2600.

It must not be concluded that polyploid genera are necessarily the most advanced in a family or tribe. Two evolutionary consequences of polyploidy are recognized. It broadens the immediately available range of variability and allows rapid adaptation to special or new habitats, and it may be responsible for "bursts" of speciation. On the other hand, it has a conservative effect on progressive evolution (Stebbins 1950), since it reduces the frequency of expression of recessive genes, and lowers the efficiency of selection. Consequently, old-established polyploids are more likely to retain primitive morphological characters than are their diploid relatives. It is suggested that in natural taxonomic groups, species or genera previously considered primitive may sometimes prove to be polyploid and their more "advanced" diploid relatives may be diploid. This inverse relationship between ploidy and primitiveness seems probable in the genus *Leucopogon* (Smith-White, unpublished data).

Escape from the conservative effects of polyploidy may follow from a process of rediploidization. Provided heterogenetic pairing does not occur between the reduplicated chromosome sets in an allopolyploid, the action of selection on random mutation in each set should result in their gradual differentiation. The process, however, must be slow, so that it modifies, but does not remove evolutionary conservatism. In amphidiploid species in *Triticum, Nicotiana,* and *Gossypium* there is little evidence of any rediploidization, and the reduplicated chromosome sets retain the genoms of their diploid parent species. The more intensively studied amphidiploids are cultivated plants, or close relatives of cultivated plants, and all are relatively recent in origin compared with the generic polyploidy inferred in the Boronieae. The development of a substantial degree of rediploidization may well be beyond the scope of genetic investigation.

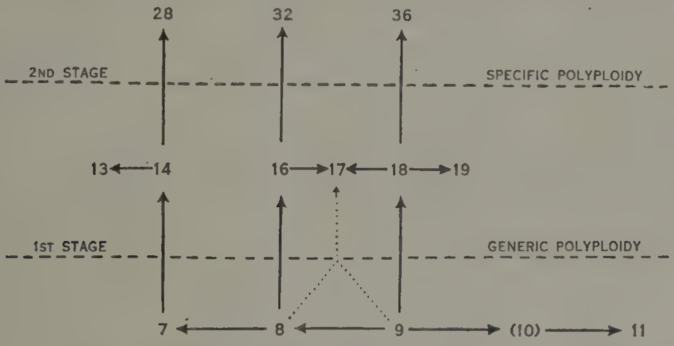


Fig. 54.—Chromosome number relationships in the Boronieae.

(*b*) *Historical Development*

Before the bearing of these inferences on the taxonomy of the group is considered, they may be extended in the light of evidence from geographical distribution. It is generally agreed that a part of the Australian flora, representing an autochthonous or paleoaustralian element, is of very ancient establishment in the continent, and that it has been isolated from other continental floras during the whole of the Tertiary period. Dispute on the source of this element—whether it is related to and derived from a paleotropical flora (Diels 1934), or whether it is Antarctic in origin — is not immediately relevant. An earlier belief

(Woolls 1884) that it had a centre of origin and primary centre of dispersal in south-western Australia is now less favoured than the hypothesis of the existence of an early pan-Australian flora (Herbert 1928, 1932). In a review of this problem on the basis of climatic, pedological, and floristic data, Crocker and Wood (1947) support the latter view, and conclude that in the Eocene genera such as *Eucalyptus, Banksia, Hakea,* and *Persoonia* were already established on a pan-Australian basis. In the Miocene, warmer climates pushed this Australian element southwards, and at the same time there was an incursion of the sea northwards from the head of the Bight for a considerable distance. Thus the Australian element was divided into eastern and western parts, and the isolation of these parts has been maintained from the Miocene to the present time in turn by physiographic, edaphic, and climatic barriers.

The Boronieae can provide no direct support for this hypothesis, since fossil remains of the group are unknown. However, the sharp specific and even generic distinction between the south-western and eastern-northern floristic regions, described earlier, suggests that two periods may be recognized in the development of the tribe in Australia — a first, in a pan-Australian flora, when the main genera were established, and a second, subsequent to the floristic bisection of the continent, during which the present specific diversity was developed. Genera which are at present common to both regions must have been established prior to the Miocene. On the other hand, genera which are at present endemic to either the eastern or western regions may be more recent in origin, or, more probably, are ancient and relic, never having expanded their ranges far from their own centres of origin. Even in a pan-Australian Eocene flora, it is not to be assumed that all "species" of that time, which may have given the genera of the present, were uniformly widespread over the continent. The genus *Zieria,* however, which is apparently wholly polyploid and is restricted to the eastern region, could be post-Miocene in origin, and in such event would be younger than some sections of *Boronia.*

There is an obvious correlation between the viewpoint expressed in the present section and the inferences which have been drawn from the cytological data. The following sequence of events has apparently taken place in the evolution of the Boronieae.

Entering Australia in very early times, probably during the Cretaceous period, together with other paleoaustralian lineages, the protoboronieae stock became isolated from other continental floras. Very probably, as suggested by Diels, they were derived from paleotropical Xanthoxyleae. The few chromosome determinations published indicate that the present-day Xanthoxyleae are highly polyploid on the basic number 9, and they may be very conservative in evolutionary change. After their isolation, the Boronieae suffered a change in chromosome structure, possibly involving an accumulation of heterochromatin close to the centromeres. The fundamental change would have occurred during a period of geographical expansion, when selection pressures must have been low, and when conditions would have been favourable to the survival of chromosomal variants. Variants from 9 to 8, 7 and 11, and polyploids on these numbers, were established. During the subsequent period (Eocene), there were "bursts" of specific radiation, so that the new numbers tend to be representative of genera rather than of species in the modern flora. With an increasing severity of selection due to a more intensive occupation of the area (Wright 1949), there was a stabilization of types, and perhaps a rediploidization of the polyploids. At a much later time, after the floristic division of the continent in the Miocene, a second stage in polyploidy occurred in most genera, and this later stage is characteristic of the species level only. The rediploidization of the earlier stage of polyploidy was perhaps necessary before the second stage could materialize. Octoploid species are relatively rare in nature, and a fourfold replication of genoms must prove unwieldy.

The existence of polyploids within species, and particularly in examples of the type found in *Boronia crassifolia*, suggest still more recent origins of the polyploid condition. Changes in climate and physiography during the Pliocene and Pleistocene epochs would offer new and altered habitats, a condition favourable to the establishment of polyploids. A decrease in aridity over the last 10,000 years or less, demanded by Crocker and Wood (1947) would permit a spread from refuges, a reduction in selection pressure, and the meeting of previously disjunct species. Such conditions must have favoured the origin of recent polyploids.

(*c*) *Taxonomy*

Bentham (1863) recognized 15 genera of the Boronieae in Australia. Engler's view (Engler and Prantl 1931) of generic limits is comparable, but he combined *Drummondita* with *Philotheca;* Mueller (1859), however, recognized only seven genera, submerging *Phebalium, Philotheca, Crowea, Asterolasia, Microcybe, Geleznowia,* and *Drummondita* in one genus with *Eriostemon,* and reducing *Zieria* to sectional rank in *Boronia.* Maiden (1916) refused recognition to *Crowea* owing to its close relationship to *Eriostemon lanceolatus,* but otherwise followed Engler. Gardner (1931) recognized two additional small western genera.

In general, the cytological data do not support Mueller's view. It has been emphasized earlier that differences in basic chromosome number in the Boronieae rank as generic rather than as specific criteria.

Eriostemon and some of the small genera allied to it have the unique base number 14, which has occasionally been reduced to 13. *Phebalium* ($x = 16$) is clearly distinct. *Crowea* ($x = 19$) and *Eriostemon lanceolatus* ($x = 17$) are both distinct from other species of *Eriostemon,* and their close relationship to one another is reflected in their cytological constitutions.

The cytological differences between *Zieria* and *Boronia* are certainly no greater than the differences between some sections of the latter. Either *Zieria* should be reduced to sectional rank, following Mueller, or the sections of *Boronia* should be elevated to generic status. If the sections of *Boronia* were contemporary in origin (pre-Miocene) with the other genera of the tribe, the latter alternative is indicated.

Within *Boronia,* there is evidence that some of the sectional groupings need revision. Cytologically, the eastern and western *Pinnatae* are not closely related, and *B. serrulata,* which is placed with the *Terminales,* belongs with the eastern *Pinnatae.* The pinnate form of the leaf, which is present also in some species of the *Valvatae* and *Heterandreae,* is probably an ancient and primitive character in the genus, and should not be used as a sectional criterion.

A very close relationship between *Phebalium* and *Correa* is suggested by the close floral similarity of *P. ralstoni* var. and *C. alba,* and is supported by the identity in chromosome number for the two genera. *Phebalium* and *Correa* may be related at the 16-chromosome level; whether they have had a common origin with *Boronia-Valvatae* is more doubtful.

A taxonomic grouping based purely on chromosome number would be unsound. The reducing series 9-8-7 has apparently occurred twice within *Boronia,* in the *Heterandreae* and in the western *Pinnatae.* Reduction to 7, followed by polyploidy, must have been independent, and probably much earlier in origin, in the Eriostemoninae.

V. ACKNOWLEDGMENTS

Much of this work was made possible by University Research Fund grants in 1950 and 1952. Grateful acknowledgment is made to Dr. B. J. Grieve and the staff of the Botany Department, University of Western Australia, for the use of the facilities of that Department and for personal assistance, and to Mr. J. Harding, of the Forestry Department, Perth, for a great deal of help in field work.

VI. REFERENCES

BABCOCK, E. B. (1947).—The genus *Crepis.* 1. *Univ. Calif. Publ. Bot.* **21.** 170 pp.

BEAL, J. M., and OWNBY, M. (1943).—Cytological studies in relation to the classification of the genus *Calochortus.* III. *Bot. Gaz.* **104:** 553-62.

BENTHAM, G. (1863).—"Flora Australiensis." (Lovell Reeve and Co.: London.)

BOWDEN, W. M. (1945).—A list of chromosome numbers in the higher plants. I. Acanthaceae to Myrtaceae. *Amer. J. Bot.* **32:** 81-92.

CROCKER, R. L., and WOOD, J. G. (1947).—Some historical influences on the development of the South Australian vegetation communities and their bearing on concepts and classification in ecology. *Trans. Roy. Soc. S. Aust.* 71: 91-136.

DARLINGTON, C. D. (1937).—"Recent Advances in Cytology." 2nd Ed. (Churchill: London.)

DARLINGTON, C. D., and JANAKI, AMMAL, E. K. (1944).—"A Chromosome Atlas of Cultivated Plants." (Allen & Unwin: London.)

DIELS, L. (1934).—Die flora Australiens und Wegeners Verschiebungs-Theorie. *S.B. preuss. Akad. Wiss.* **1934**: 533-45.

DIELS, L. (1936).—The genetic phytogeography of the South Western Pacific area with particular reference to Australia. *In* "Essays in Geobotany in honour of W. A. Setchell." (Univ. Calif. Press: Berkeley.)

ENGLER, A., and PRANTL, K. (1931).—"Die naturlichen Pflanzenfamilien." Vol. 19a: 187-359. (W. Engelmann: Leipzig.)

GARDNER, C. A. (1931).—"Enumeratio Plantarum Australiae Occidentalis." (Govt. Printer: Perth.)

HAKANSSON, A. (1946).—Meiosis in hybrid nullosomics and certain other forms of *Godetia whitneyi*. *Hereditas, Lund* **32**: 495-513.

HERBERT, D. A. (1928).—The major factors in the present distribution of the genus *Eucalyptus*. *Proc. Roy. Soc. Qd.* **40**: 165-93.

HERBERT, D. A. (1932).—The relationships of the Queensland flora. *Proc. Roy. Soc. Qd.* **44**: 2-22.

MAIDEN, J. H. (1916).—"A Census of New South Wales Plants." (Govt. Printer: Sydney.)

MUELLER, F. (1859).—"Fragmenta Phytographiae Australiae." (Govt. Printer: Melbourne.)

SHERMAN, M. (1946).—Karyotype evolution: a cytogenetic study of seven species and six interspecific hybrids in *Crepis*. *Univ. Calif. Publ. Bot.* 18: 369-408.

SMITH, W. W. (1933).—Some aspects of the bearing of cytology on taxonomy. *Proc. Linn. Soc. Lond.* **145**: 151-81.

STEBBINS, G. L. JR. (1950).—"Variation and Evolution in Plants." (Columbia Univ. Press: New York.)

TOBGY, H. A. (1943).—A cytological study of *Crepis fuliginosa* and *C. neglecta* and their F_1 hybrid and its bearing on the mechanism of phylogenetic reduction in chromosome number. *J. Genet.* 45: 67-111.

WOOLLS, W. (1884).—On the Myrtaceae of Australia. *Proc. Linn. Soc. N.S.W.* **9**: 641-8.

WRIGHT, S. (1949).—Adaptation and selection. *In* "Genetics, Paleontology and Evolution." pp. 365-89. (Princeton Univ. Press: N.J.)

OBJECTIVE METHODS FOR THE CLASSIFICATION OF VEGETATION

III. AN ESSAY IN THE USE OF FACTOR ANALYSIS*

By D. W. Goodall†

(*Manuscript received April* 5, 1954)

Summary

The possibilities of using the statistical technique of factor analysis in describing variations in plant communities are explored. This method enables the variations to be treated as continuous, instead of resulting in a separation of the stands studied into a limited number of discrete associations or other synecological categories. It further provides a means for testing whether such separation can be objectively justified. It may often facilitate the recognition of the complexes of environmental factors which mainly determine differences in vegetation, and provides a means of estimating the relative value of the various species as indicators of these environmental complexes.

In the present paper, the "principal axes" technique of factor analysis is applied to the analysis of data for percentage cover for 14 species in the Victorian Mallee. It is shown that their distribution, in so far as it does not depend on factors peculiar to individual species, can be represented in terms of at most five orthogonal "factors". The two most important "factors" are interpreted in terms of catenary changes in the vegetation. Other less common species not included in the analysis show high correlations with these "factors". In units of 1.28 ha there is no evidence that more than one continuously varying population is represented in the area; but in units of 25 sq. m. the majority of quadrat records fall into one or other of two principal categories, representing the valley and ridge communities. The potential value of factor analysis in plant sociology, and difficulties in its application to this field, are discussed.

I. Introduction

Whenever the classification of vegetation, taking into account the presence and quantity of more than one or two species, is considered, ideas of interspecific correlation are always involved tacitly, if not explicitly. In the work of the Zurich-Montpellier school, for instance (see Goodall 1952), they remain tacit. They became explicit in such investigations as those of Kulczynski (1927) and Sørensen (1948); Tuomikoski (1942) attempted actually to use product-moment correlations to designate axes in a continuum, in which vegetational records could be placed in order according to their specific composition. The present series of papers continues this line of thought, and endeavours to make use of statistical tools better than those available to the earlier investigators.

---

* A paper embodying some of the material in the present publication was read at the International Biometric Conference in Bellagio, Italy, on September 4, 1953.

† At the time the field observations were made, the author was on the staff of the University of Melbourne. His present address is Department of Agricultural Botany, University of Reading, England.

In the first paper of this series (Goodall 1953*a*) reasons were given for regarding the lack of correlations between the quantities of species present in sample areas as evidence of the homogeneity of the area sampled, and a method was described by which a heterogeneous collection of quadrat data could be. divided into groups answering to this criterion of homogeneity. It was indicated that this treatment was regarded as no more than an approximation; that it divided into discrete groups what should probably be regarded as regions in a single continuum, without any natural boundaries. It is the purpose of the present paper to conduct a preliminary exploration of a method which enables the features of this postulated continuum to be studied. Until this has been done, it does not seem possible to test the appropriateness of these two methods of treatment respectively.

The first and simplest hypothesis to be tested is that the collection of data is homogeneous, and that the variations in it can be regarded as arising from random causes only, there being no correlation between the quantities of the various species present; let us call this hypothesis A. If hypothesis A has to be rejected, the simplest hypothesis which may still be tenable would appear to be that the data arise from a single population, the non-random variations found in which can be ascribed to correlations among the species; this will be called hypothesis B. Such correlations will usually depend on some overriding environmental factors which are not uniform over the area studied; but the existence of such factors is not hypothesis B, and to test it directly would require environmental as well as vegetational data. Almost equal in simplicity to hypothesis B is the supposition (hypothesis C) that the observational data sample a number of discrete populations, within each of which the variables are subject only to random variation; this is the hypothesis tacitly accepted as the background to most systems for the classification of vegetation. The way to test hypothesis C lies through hypothesis B. The simplest forms of these hypotheses — namely, that there is a single population showing a single set of interdependent correlations among the species, or that there are just two separate populations without internal interspecific correlations — will be called respectively hypotheses B_1 and C_1.

Considered geometrically, the records for each sample area of the quantities of each species, after standardization, may be regarded as specifying a point in a coordinate system of as many axes as there are species. If a single homogeneous population is concerned, the points for the various sample areas will form a single hyper-spherical cluster. If hypothesis B_1 is justified, the points will again fall into a single cluster, but the shape of this cluster will be that of a hyper-ellipsoid rather than a hyper-sphere, one axis being elongated while the others remain equal. If, on the other hand, hypothesis C_1 is true, the points will form two separate hyper-spherical clusters. Now if hypothesis C_1 is true, but hypothesis B_1 is provisionally accepted, the process of identifying the vector corresponding to the long axis of the postulated hyper-ellipsoid will in fact give the vector joining the centres of the two hyper-spherical clusters. If then the distribution along this vector of the projections of the points be studied, they will be found to be distributed bimodally, and this bimodality provides evidence supporting hypothesis C_1 against hypothesis B_1. This argument can, of course, be extended to the more general hypotheses B and C.

If a hypothesis of separate populations of the general form of hypothesis C is accepted, discriminant analysis (Goodall 1953*b*) forms the appropriate method of treatment of the observational data, particularly where questions such as the allocation of intermediate points are being considered. But if factorial hypotheses such as B are being tested — if, that is, a hypothesis of separate populations has not yet been proved — the methods of factor analysis are appropriate.

Factor analysis is a technique developed in the first instance — primarily by Spearman (1927) — for the treatment of psychological data. In the testing of intelligence and ability, the psychologist is confronted with a mass of data consisting of the scores of a number of individuals in each of a battery of tests; from these data he wishes to draw conclusions as to the general intelligence of each individual, and as to any particular abilities independent of general intelligence which have affected the results of the tests. The methods developed by Spearman and by the psychologists and statisticians who studied the question afterwards enabled the original mass of data, too extensive to be readily grasped as it stood, to be simplified so that the collection of scores for each individual could be represented by a single figure expressing "general intelligence", or a small group representing particular abilities. When these general factors had been removed from the test scores, the residuum of variation depended only on factors peculiar to each test.

The analogy between this situation in psychology and that with which the plant sociologist is confronted is close. For intelligence tests, one reads plant species; for individuals under test, one reads sample areas; for test scores, the quantity of the species present; for general intelligence or particular abilities, one may substitute xerophytism, salinity tolerance, nutritional requirements, and the like. And, just as the general intelligence shown by the test scores of a child may depend on his genetic constitution, the diseases he has suffered, and his nutrition, so the general level of xerophytism of the plants growing in a sample area will depend on its soil and subsoil structure, rainfall, slope, evaporation, and so forth.

Various techniques have been used for factor analysis (see Holzinger and Harman 1941). Of these techniques, that first described by Hotelling (1933) and termed the method of "principal axes" lends itself best to tests of significance, although the computing work is somewhat heavier than with other techniques. The appropriate significance tests have been discussed by Bartlett (1950), and the method of "principal axes", with these tests, has been used in the present work.

TABLE 1

CORRELATIONS BETWEEN PERCENTAGE COVER (AFTER ANGULAR TRANSFORMATION) FOR 14 SPECIES OF PLANTS IN THE VICTORIAN MALLEE

	B. uniflora	*C. pseudomicrophyllum* (prostrate form)	*C. pseudomicrophyllum* (erect form)	*D. semiannularis*	*D. bursariifolia*	*E. calycogona*	*E. dumosa*	*E. oleosa*	*M. uncinata*	*S. variabilis*	*T. irritans*	*V. triloba*	*W. rigida*	*Z. apiculatum*
Bassia uniflora (R.Br.) F. Muell.	1.000	0.174	0.095	—0.510	—0.603	0.328	—0.471	0.601	—0.431	0.254	—0.628	0.032	0.213	0.683
Chenopodium pseudomicrophyllum Aellen (prostrate form)	0.174	1.000	0.271	—0.129	—0.335	0.307	0.119	0.047	—0.270	0.393	—0.157	0.400	0.120	0.025
C. pseudomicrophyllum (erect form)	0.095	0.271	1.000	0.309	0.058	0.208	0.255	0.197	—0.181	0.616	—0.166	0.060	0.090	—0.009
Danthonia semiannularis R.Br.	—0.510	—0.129	0.309	1.000	0.449	—0.115	0.295	—0.382	0.377	0.265	0.270	0.198	—0.263	—0.450
Dodonaea bursariifolia Behr.	—0.603	—0.335	0.058	0.449	1.000	—0.325	0.456	—0.419	0.327	—0.074	0.547	—0.295	—0.298	—0.508
Eucalyptus calycogona Turcz.	0.328	0.307	0.208	—0.115	—0.325	1.000	0.072	0.059	—0.654	0.366	—0.220	0.001	0.400	0.327
E. dumosa A. Cunn.	—0.471	0.119	0.255	0.295	0.456	0.072	1.000	—0.512	—0.044	—0.036	0.469	0.199	—0.186	—0.542
E. oleosa F. Muell.	0.601	0.047	0.197	—0.382	—0.419	0.059	—0.512	1.000	—0.499	0.194	—0.688	—0.056	0.224	0.586
Melaleuca uncinata R.Br.	—0.431	—0.270	—0.181	0.377	0.327	—0.654	—0.044	—0.499	1.000	—0.183	0.412	0.154	—0.478	—0.427
Stipa variabilis Hughes	0.254	0.393	0.616	0.265	—0.074	0.366	—0.036	0.194	—0.183	1.000	—0.372	0.239	0.128	0.163
Triodia irritans R.Br.	—0.628	—0.157	—0.166	0.270	0.547	—0.220	0.469	—0.688	0.412	—0.372	1.000	—0.200	—0.206	—0.399
Vittadinia triloba D.C.	0.032	0.400	0.060	0.198	—0.295	0.001	0.199	—0.056	0.154	0.239	—0.200	1.000	—0.151	—0.013
Westringia rigida R.Br.	0.213	0.120	0.090	—0.263	—0.298	0.400	—0.186	0.224	—0.478	0.128	—0.206	—0.151	1.000	0.285
Zygophyllum apiculatum F. Muell.	0.683	0.025	—0.009	—0.450	—0.508	0.327	—0.542	0.586	—0.427	0.163	—0.399	—0.013	0.285	1.000

For $P = 0.05$, $r = 0.349$.

II. The Observational Data and Their Analysis

(*a*) *The Original Data*

The collection of data to which factor analysis was first applied was that from the Victorian Mallee, which has already been used in other connexions (Goodall 1953*a*, 1953*b*). Information was available on the percentage cover by each species of flowering plant in each of 256 quadrats of 25 sq. m. area distributed by restricted randomization within an area of 640 m square occupied by virgin mallee scrub vegetation. Of the 57 species recorded, the 14 most frequent (all, that is, recorded in more than 20 quadrats), including the two distinct forms of *Chenopodium pseudomicrophyllum,* were selected for study.

Table 2

JOINT DISTRIBUTION OF PLANTS IN THE VICTORIAN MALLEE: FACTOR COEFFICIENTS

Species	Factor *A*	Factor *B*	Factor *C*	Factor *D*	Factor *E*
Bassia uniflora	0.838	—0.102	0.142	—0.023	—0.104
Chenopodium pseudomicrophyllum (prostrate form)	0.309	0.574	0.086	0.494	—0.122
C. pseudomicrophyllum (erect form)	0.150	0.726	0.022	—0.466	—0.175
Danthonia semiannularis	—0.556	0.480	0.224	—0.333	0.323
Dodonaea bursariifolia	—0.740	0.077	—0.217	—0.414	—0.159
Eucalyptus calycogona	0.502	0.432	—0.502	0.156	0.231
Eucalyptus dumosa	—0.534	0.529	—0.335	0.232	—0.386
Eucalyptus oleosa	0.759	—0.152	0.176	—0.347	—0.307
Melaleuca uncinata	—0.674	—0.206	0.553	—0.020	0.259
Stipa variabilis	0.343	0.723	0.209	—0.327	0.190
Triodia irritans	—0.760	—0.057	—0.342	0.149	0.088
Vittadinia triloba	0.045	0.431	0.590	0.520	0.052
Westringia rigida	0.479	0.056	—0.509	0.004	0.437
Zygophyllum apiculatum	0.768	—0.223	0.017	—0.077	0.117

To reduce the volume of the data, and the number of zero values, the quadrat records were first combined in groups of eight. Since the area studied had first been divided into an 8 by 8 grid, this means that the units for the factor analysis consisted of rectangles 160 by 80 m, in each of which values for eight quadrats were available; the means of these groups of eight values were the data used in the analysis.

(*b*) *The Correlation Matrix and its Analysis*

The percentage cover data were first subjected to angular transformation; for each pair of species, the product-moment correlation coefficients between these transformed data were then computed. The resulting correlation matrix is shown in Table 1. It will be noted that, of the 91 correlations, 32 reach the 5 per cent. level of significance. The initial test of the determinant of the whole matrix (Bartlett 1950), as might be expected, showed significance at an extremely high level, with $\chi^2 = 238.4$ ($n = 91, P < 10^{-15}$), so that the hypothesis of homogeneity was definitely unacceptable.

A first factor, corresponding to the longest axis of the postulated hyper-ellipsoid, was accordingly extracted; this will be termed factor A. It accounted for a substantial part of the correlations observed, for the corresponding latent root was 4.760 (as against a mean of unity for all 14 latent roots of the matrix). The factor coefficients* for the 14 species are shown in the second column of Table 2. It will be noted that the species with the highest positive coefficients for factor A are *Bassia uniflora, Zygophyllum apiculatum,* and *Eucalyptus oleosa,* while high negative coefficients occur with *Triodia irritans, Dodonaea bursariifolia,* and *Melaleuca uncinata.* It is thus clear that factor A may be regarded as representing adaptation to poorer drainage and the other conditions that go with it, for the first group of species is found in the hollows that run from east to west across the area, while the other group is found on the intervening ridges. This is illustrated in Figure 1(*b*), where the values of factor A for each of the quadrat groups are shown in their appropriate positions on a plan of the area; it may be compared with the contour map in Figure 1(*a*).

A test of the claims of hypotheses B_1 and C_1 is now possible. In Figure 2 the frequency distribution of the values of factor A for different quadrat groups has been plotted as a histogram. There seems from this diagram no *prima facie* evidence of the existence of two discrete types of vegetation in the area, and a test of deviations from normality (though, of course, insensitive with only 32 observations) gave a value for χ^2 of 1.75 (with 3 degrees of freedom, the distribution being divided for this purpose at the pentiles). Hypothesis C_1 may thus be rejected.

The existence of this common factor A by no means accounted for the whole of the interspecific correlations; when the determinant of the residual matrix after its elimination was tested, it still gave a significant value of χ^2 (see Table 3). A second factor (factor B) was accordingly extracted.

The coefficients of this second factor are shown in the third column of Table 2. Here, the highest coefficients are those for *Stipa variabilis* and *Chenopodium pseudomicrophyllum,* and the lowest those for *Zygophyllum apiculatum* and *Melaleuca uncinata.* This is much more difficult to interpret in terms of adaptational features than factor A, for there seems little in common between *Z. apiculatum* and *M. uncinata* — and, in fact, they initially showed a strong negative correlation. However, if dot diagrams are prepared to show the relationship between the quantities of the individual species and the values of factor A, the significance of factor

---

* These factor coefficients give the direction ratios of the vector corresponding to the longest axis of the hypothetical hyper-ellipsoid; their actual magnitudes are such as to provide the coordinates of a point on the vector distant from the origin by an amount equal to the standard deviation of the factor.

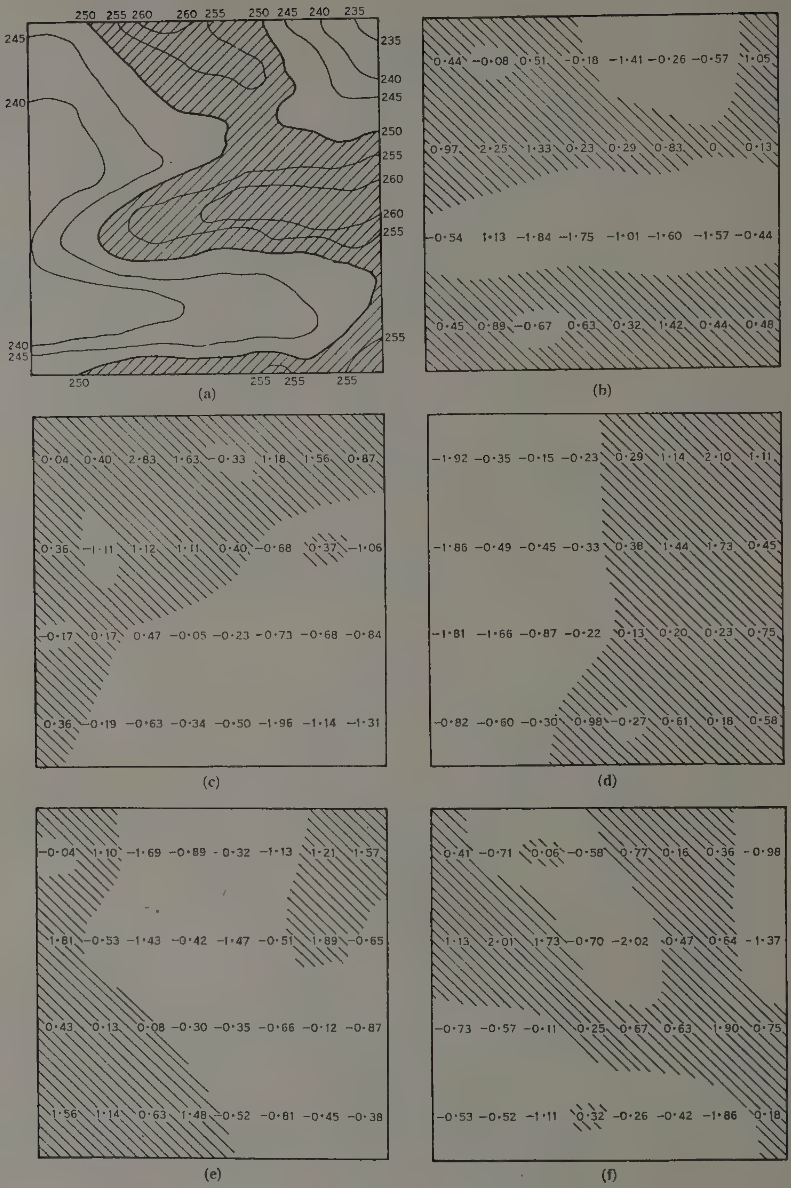

250 255 260 260 255 250 245 240 235
245
240
235
240
245
250
255
260
260
255
255
240
245
250 255 255 255
(a)
0·44 −0·08 0·51 −0·18 −1·41 −0·26 −0·57 1·05
0·97 2·25 1·33 0·23 0·29 0·83 0 0·13
−0·54 1·13 −1·84 −1·75 −1·01 −1·60 −1·57 −0·44
0·45 0·89 −0·67 0·63 0·32 1·42 0·44 0·48
(b)
0·04 0·40 2·83 1·63 −0·33 1·18 1·56 0·87
0·36 −1·11 1·12 1·11 0·40 −0·68 0·37 −1·06
−0·17 0·17 0·47 −0·05 −0·23 −0·73 −0·68 −0·84
0·36 −0·19 −0·63 −0·34 −0·50 −1·96 −1·14 −1·31
(c)
−1·92 −0·35 −0·15 −0·23 0·29 1·14 2·10 1·11
−1·86 −0·49 −0·45 −0·33 0·38 1·44 1·73 0·45
−1·81 −1·66 −0·87 −0·22 0·13 0·20 0·23 0·75
−0·82 −0·60 −0·30 0·98 −0·27 0·61 0·18 0·58
(d)
−0·04 1·10 −1·69 −0·89 −0·32 −1·13 1·21 1·57
1·81 −0·53 −1·43 −0·42 −1·47 −0·51 1·89 −0·65
0·43 0·13 0·08 −0·30 −0·35 −0·66 −0·12 −0·87
1·56 1·14 0·63 1·48 −0·52 −0·81 −0·45 −0·38
(e)
0·41 −0·71 0·06 −0·58 0·77 0·16 0·36 −0·98
1·13 2·01 1·73 −0·70 −2·02 0·47 0·64 −1·37
−0·73 −0·57 −0·11 0·25 0·67 0·63 1·90 0·75
−0·53 −0·52 −1·11 0·32 −0·26 −0·42 −1·86 0·18
(f)

Fig. 1.—Maps of area under study: (*a*), Contour map; (*b*) factor *A*; (*c*) factor *B*; (*d*) factor *C*; (*e*) factor *D*; (*f*) factor *E*. In (*a*) the area more than 250 ft above sea-level has been shaded; in (*b*) to (*f*) the areas shaded are those with positive values for the factor in question.

B becomes clear. This has been done in Figure 3. Whereas *C. pseudomicrophyllum* and *Stipa variabilis* show a marked maximum towards the centre of the range of factor *A*, the relationships in *M. uncinata* and

Z. apiculatum are practically linear, decreasing and increasing respectively with increasing values of factor *A*. Thus factor *B* simply represents a non-linear component of the relationship of the distribution of the species to factor *A*. To put it in adaptational terms, if factor *A* represents adaptation to conditions of restricted drainage (species with large negative coefficients being poorly adapted to conditions of restricted drainage, but well adapted to free drainage), then species best adapted to intermediate drainage conditions but growing poorly under either extreme of restricted or free drainage will have coefficients close to zero for factor *A*, but high positive coefficients for factor *B*.

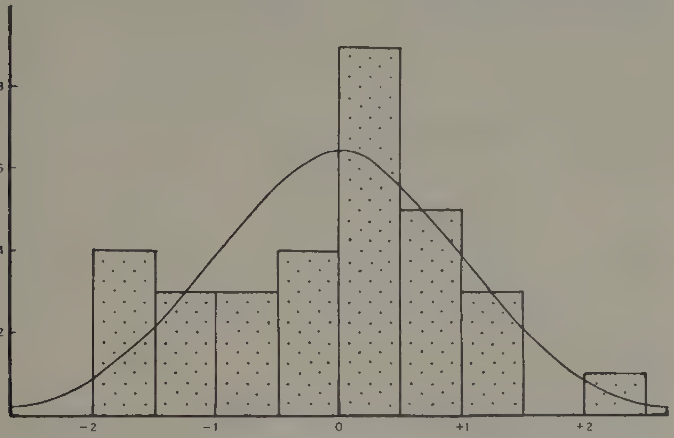


Fig. 2.—Frequency polygon (with fitted normal curve) for values of factor *A*, groups of eight quadrats.

TABLE 3

LATENT ROOTS OF CORRELATION MATRIX CORRESPONDING TO SIGNIFICANT FACTORS

Factor	Latent Root	χ^2	n	P
A	4.760	238.4	91	$<10^{-15}$
B	2.399	153.0	78	$<10^{-6}$
C	1.595	114.3	66	0.0005
D	1.348	88.6	55	0.002
E	0.801	63.9	45	0.03
Sum for all others	3.097	29.9	36	0.75

In view of this interpretation of factor *B*, it is not surprising that the spatial distribution of positive and negative values of this factor is irregular (Fig. 1(*c*)), showing little correlation with any topographical features. Factor *B* also provides no evidence that the population is multiple; Figure 4 shows, in the form of a dot diagram, the joint distribution of values for factors *A* and *B* — and no signs of clumping can be seen.

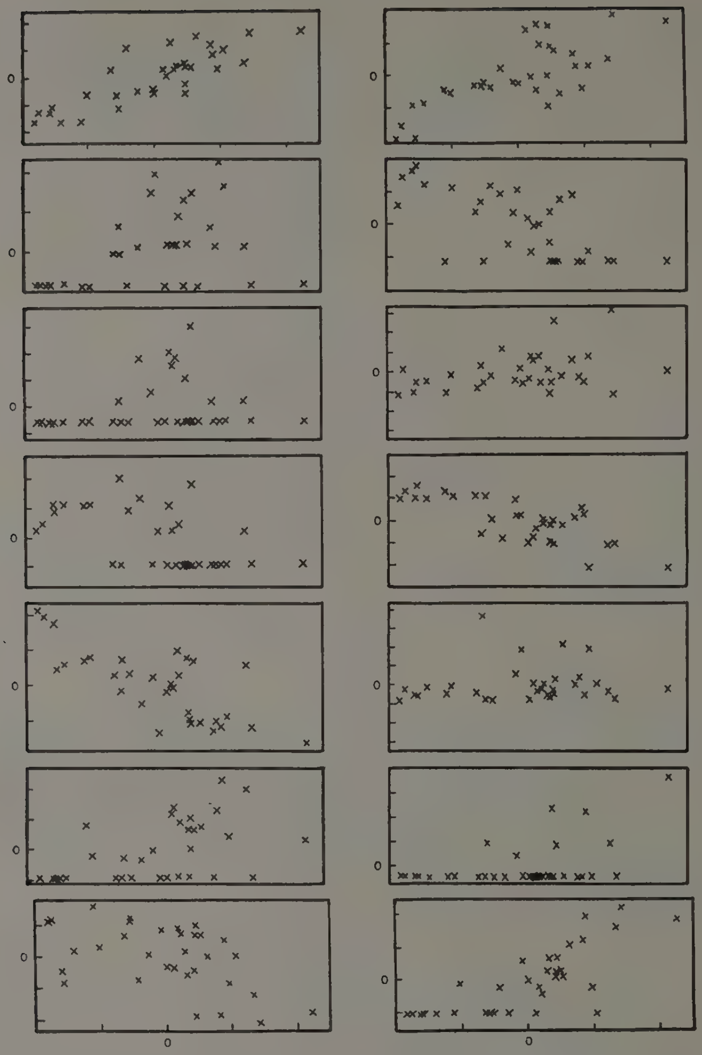


Fig. 3.—Quantity of each species (angular transform of percentage cover) corresponding to different values of factor *A*:

Bassia uniflora
Chenopodium pseudomicrophyllum
(prostrate form)
C. pseudomicrophyllum
(erect form)
Danthonia semiannularis
Dodonaea bursariifolia
Eucalyptus calycogona
E. dumosa
E. oleosa
Melaleuca uncinata
Stipa variabilis
Triodia irritans
Vittadinia triloba
Westringia rigida
Zygophyllum apiculatum

The determinant of the residual matrix after the elimination of factor *B* was still significant (see Table 3), and a third factor (*C*) was accordingly extracted. The coefficients may be seen in Table 2. Here the largest positive values are for *Vittadinia triloba* and *Melaleuca uncinata*, the largest negative ones *Westringia rigida* and *Eucalyptus calycogona*. It is again difficult to interpret this factor in terms of similarities between the species mentioned, and the distribution diagrams of Figure 3 do not suggest an explanation on the lines of that for factor *B*, based on a different set of coincident "humps". The spatial distribution of values of factor *C*, however (Fig. 1(*d*)), shows a remarkably simple pattern, all the positive values being grouped together on the east side of the area studied. On a larger scale, this would almost suggest mutual replacement by two distinct floristic elements, but in the present case this explanation would seem too far-fetched. It is conceivable, however, that a mosaic variation on a scale even larger than that giving the vegetational differences between ridges and hollows is superimposed on it, and that the area studied includes portions of two elements of this mosaic.

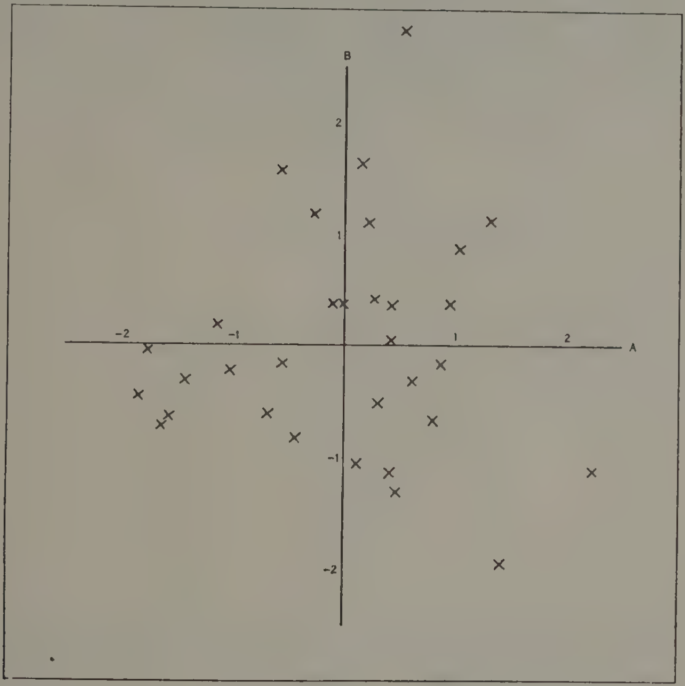


Fig. 4.—Joint distribution of factors *A* and *B*, groups of eight quadrats.

The joint distribution of values of factors *A*, *B*, and *C* cannot well be represented in two dimensions, but the joint distributions of factor *C* with factors *A* and *B* are shown separately in Figure 5(*a*), (*b*). Again, there is no clear indication that more than one population is present.

The determinant of the residual matrix of correlations remained significant (see Table 3), and a fourth factor (D) was accordingly extracted. Once again, the factor coefficients are shown in Table 2; the largest positive coefficients are those for *Vittadinia triloba* and the prostrate form of *Chenopodium pseudomicrophyllum*, the largest negative ones those for the erect form of *C. pseudomicrophyllum* and *Dodonaea bursariifolia*. Apart from the interesting distinction between the two forms of *C. pseudomicrophyllum*, it is difficult to make biological sense of this factor. Its distribution pattern in the field (Fig. 1(*e*)) is fairly simple, though not obviously related to features of relief or to the other associated environmental factors. Once again, the dot diagrams (Figs. 6(*a*), (*b*), (*c*)) indicating its joint distribution with the three factors already extracted show no clear evidence of clumping such as one would expect if the population were multiple.

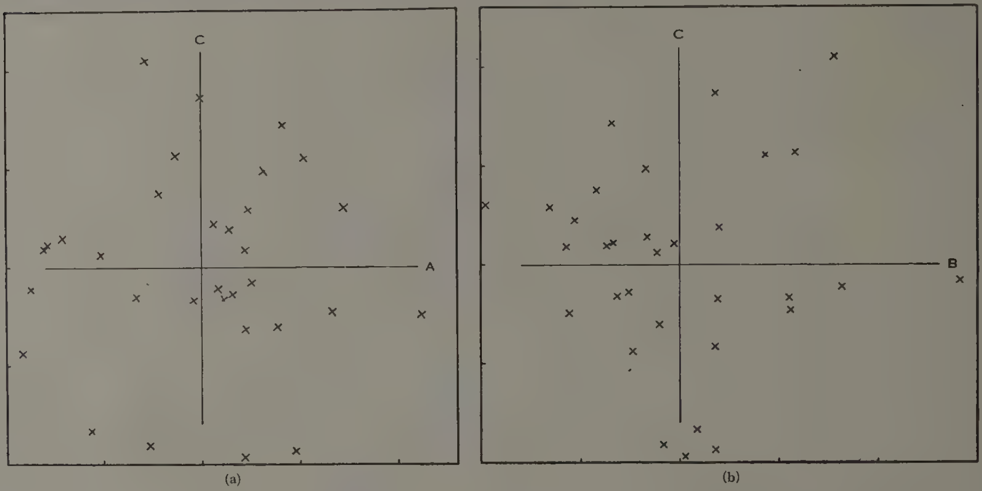
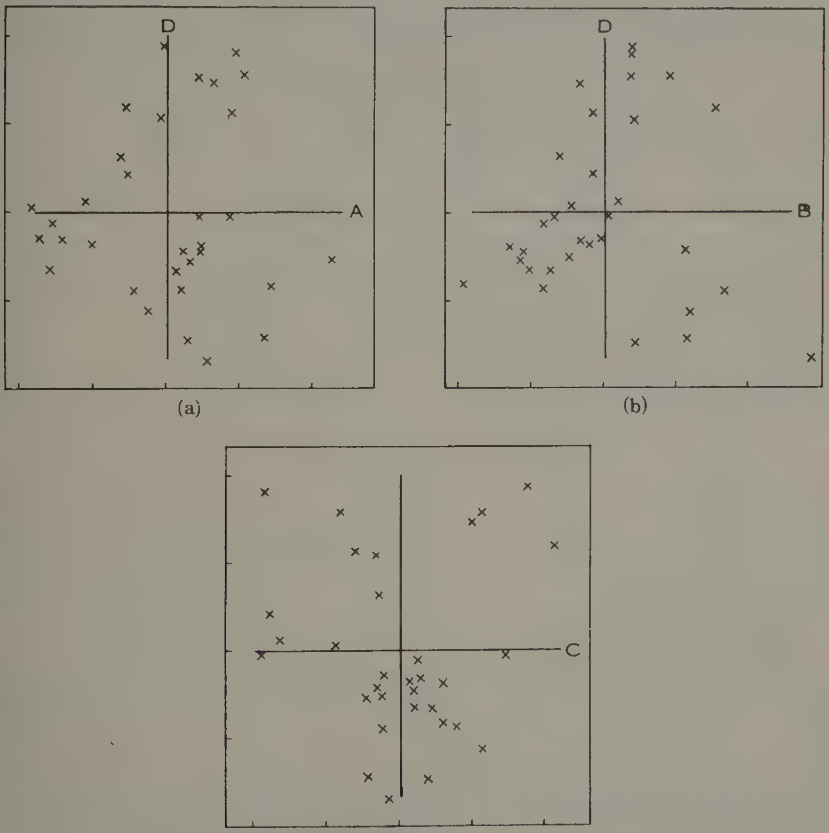


Fig. 5.—(*a*) Joint distribution of factors A and C, groups of eight quadrats. (*b*) Joint distribution of factors B and C, groups of eight quadrats.

The determinant of the residual matrix had still not been reduced to non-significance by the elimination of these four factors. It was, however, sufficiently close to the usual 5 per cent. significance level to make it doubtful whether a fifth factor should be extracted. However, a factor E was computed; the coefficients are shown in the final column of Table 2 and the distribution pattern in the field in Figure 1(*f*). After the removal of this factor, there is no reasonable doubt that factorization is complete.

(*c*) *Relevance of the Factor Analysis to Smaller Sample Areas*

It was initially stated that, for convenience of treatment and for better approximation to normality, quadrats were combined in neighbouring groups of eight, so that the units in the analysis were areas measuring 80 m in the east-west direction by 160 m from north to south, each of which had been sampled by eight 25-sq. m. quadrats under restricted randomization. The units of area were deliberately made longer from north to south since the most obvious vegetational differences were in this direction, and it was feared that otherwise these most obvious differences might overshadow and obscure any others.



(a) (b) (c)

Fig. 6.—Joint distributions of factor *D* with (*a*) factor *A*, (*b*) factor *B*, and (*c*) factor *C*, groups of eight quadrats.

Since, in most types of vegetation, variations on several scales are superimposed one upon the other, it was unlikely that the relative importance of these different types of variation would be the same for individual quadrats as for the large rectangular areas; consequently, one would not expect the results of factor analysis applied to data for individual quadrats to be exactly the same as for the groups of eight quadrats. But, if the larger-scale variations are important, they will be reflected in the factors extracted in either case, and the smaller-scale variation will simply increase the number of significant factors.

It is accordingly of interest to evaluate for individual quadrats the factors extracted for the larger rectangular areas. This has been done for factors *A*, *B*, and *C*. In Figure 7 the distribution of these values is shown for each factor separately. It is noteworthy that, for factor *A*, the distribution is clearly bimodal (for deviations from normality, $\chi^2 = 64.74$; $n = 10$; $P << 0.001$) and suggests that individual quadrats may fall into two distinct populations, the ranges of values for factor *A* overlapping somewhat. Factor *B* is unimodal, but skewed to a significant extent ($\chi^2 = 33.62$; $n = 11$; $P < 0.001$), which is probably connected with the skew distributions of some of the species contributing most strongly to this factor. The distribution of factor *C* suggests bimodality, though less strongly than in factor *A*, and in any case is not normal ($\chi^2 = 27.90$; $n = 11$; $P < 0.01$). The joint distribution of factors *A* and *B*, and *A* and *C*, are shown in Figures 8 and 9. Figure 8 shows again the bimodal distribution commented upon in relation to Figure 7(*a*); the two principal clusters of points are in fact separated by a band which is almost empty, and the points which occur between them in the one-dimensional repre-

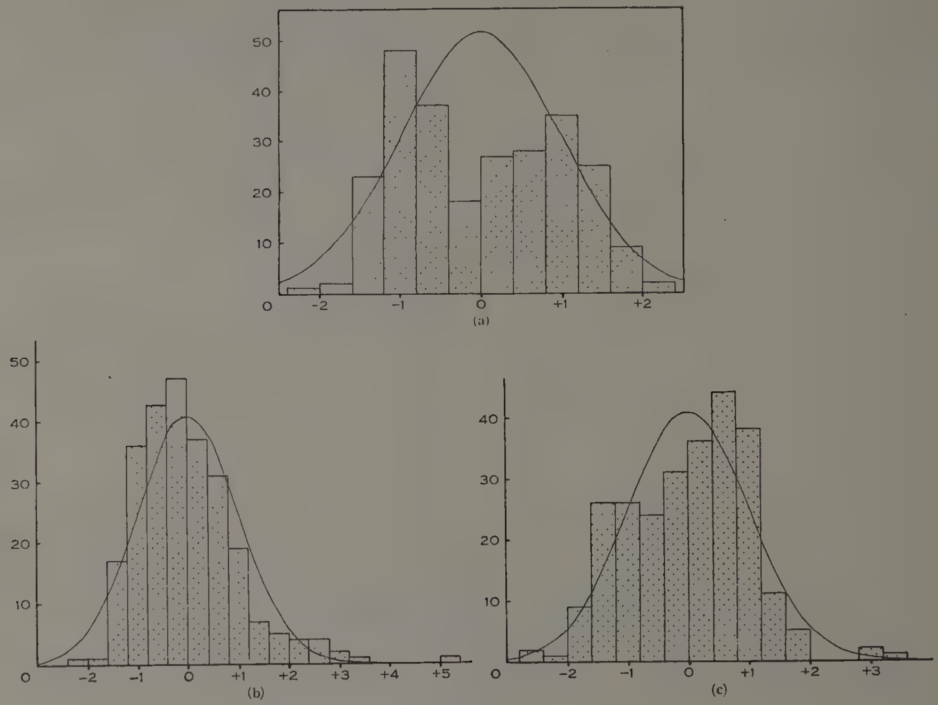


Fig. 7.—Frequency polygon (with fitted normal curve) for standardized values of (*a*) factor *A*, (*b*) factor *B*, and (*c*) factor *C*, individual quadrats.

sentation are here displaced in the positive direction of factor *B*. Thus the effective separation of the two populations has been increased by taking two factors into account, and they are now connected by a rather attenuated U-shaped band. The botanical interpretation is, of course, clear: the two clusters represent the two ends of the catena; quadrats with intermediate composition are less common, and are characterized by additional species which do not occur, or occupy less ground, at either extreme. Figure 9 shows a clearly marked cluster with positive values for both *A* and *C*, and a suggestion of distinction of two clusters with negative values of *A*, but positive and negative respectively for *C*.

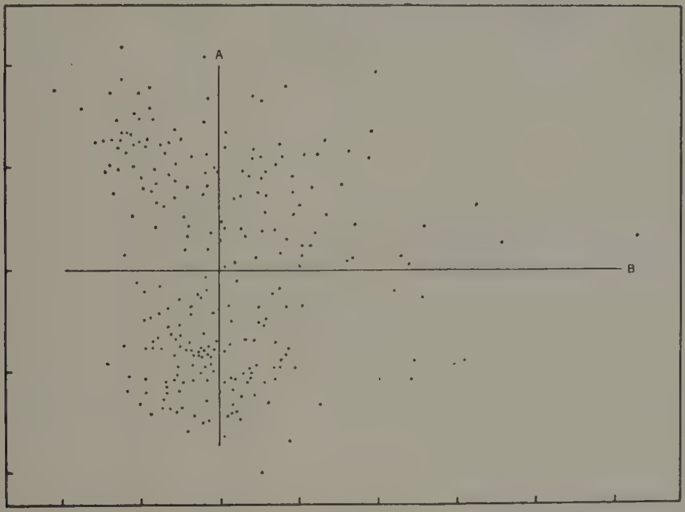


Fig. 8.—Joint distribution of factors *A* and *B*, standardized values for individual quadrats.

For factor *A*, the spatial distribution of the values for individual quadrats has been plotted in Figure 10. Comparing this with Figure 1(*b*), it is clear that combining data for quadrats in groups of eight has partially obscured the dependence of this factor on the topography of the area. The ridge community on the southern edge, for instance, is clear in Figure 10, but not shown in Figure 1(*b*).

(*d*) *Relevance of the Factor Analysis to Other Species*

Since the factor analysis computations become very unwieldy when the number of variates is large, only 14 of the 57 species recorded were included in the analysis. If, however, the results were applicable to the whole vegetation, one would expect the distribution of the other, less frequent, species to be correlated fairly closely with the values of the factors extracted from the data for the commoner species. That this is so is shown in Table 4. For this purpose, the factor values for individual quadrats have been used; a 2 × 2 table has been constructed showing the association of the species with high or low values of the factor, and tested by the χ^2 or the exact test, as appropriate. For species occurring in more than nine quadrats the factor values were divided at the median, for those occurring in from three to nine quadrats at the upper or lower quartile; species occurring in one or two quadrats only were not included.

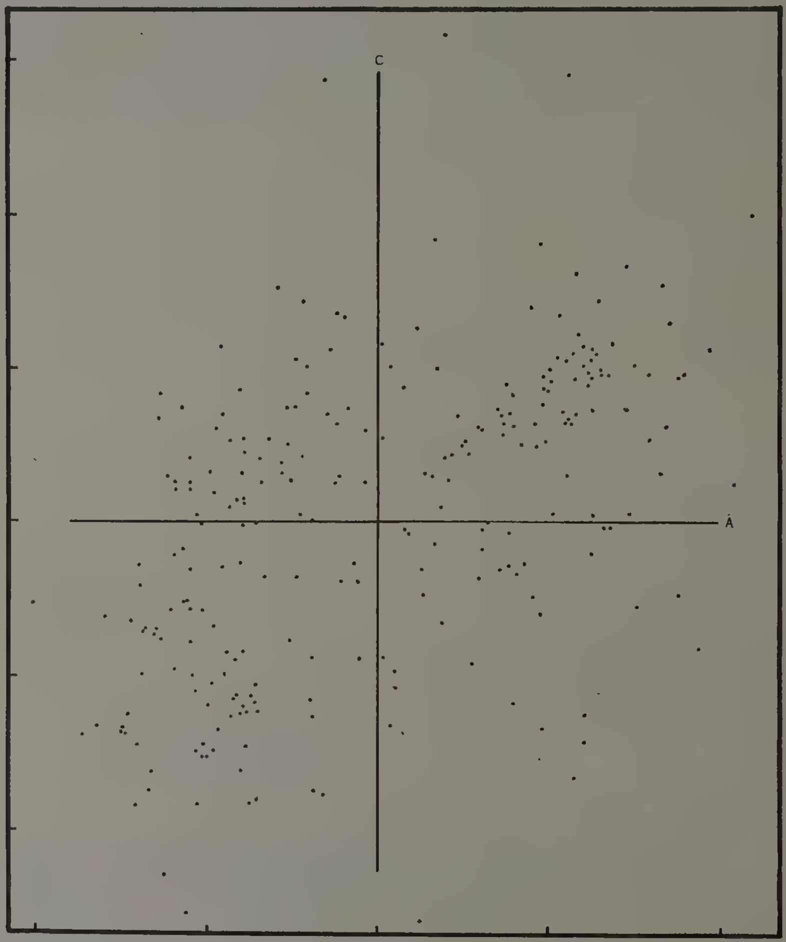


Fig. 9.—Joint distribution of factors *A* and *C*, standardized values for individual quadrats.

For factor *A*, no fewer than 12 out of the 29 species included in Table 3 show significant association, and for each factor the number of entries in the table is significantly greater than expectation.

III. DISCUSSION

This first[*] attempt to apply the methods of factor analysis to the problems of plant sociology has shown that it can display neatly and conveniently many of the relationships subsisting between the distribution of different species; but it has also shown that there are a number of obstacles to be surmounted before it can be regarded as a fully appropriate instrument for this purpose.

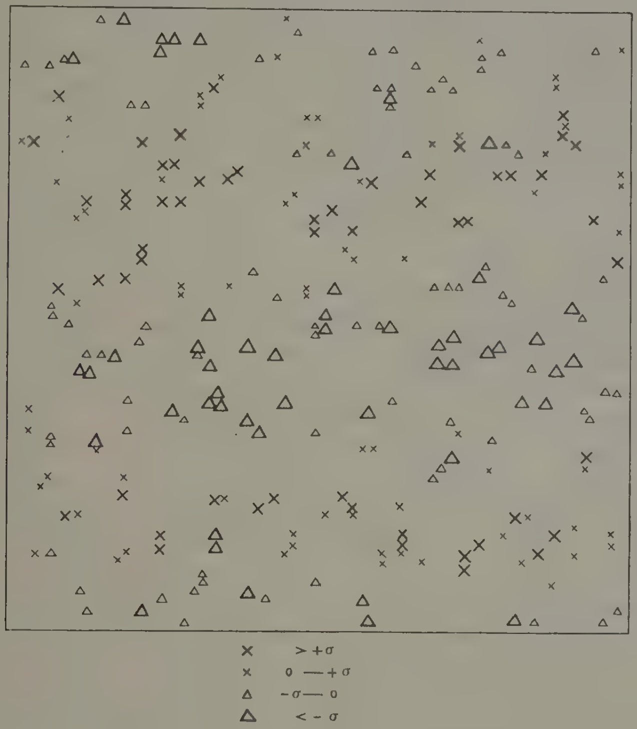


Fig. 10.—Map of area, showing distribution of values of factor *A* for individual quadrats.

The most important difficulty revealed in this study is the non-linear relationship of the distribution of several species to the factors extracted. This does not invalidate the analysis, for it is still true that the number of factors extracted indicates the number of independent terms required adequately to specify for any quadrat the quantities of the various species expected, in so far as this does not depend on features peculiar to the one species. But it means that, though the factors may be statistically orthogonal, they are not biologically independent; the interpretation thus becomes more complicated.

---

[*] When a paper based on this was read at the Third International Biometric Conference, I was interested to learn that work on similar lines at Wageningen was approaching completion. Data collected for grassland communities by Dr. D. M. de Vries were being analysed by Dr. G. Hamming. It seems probable that the results of this work will be published at about the same time as the present paper.

TABLE 4

SIGNIFICANCE OF ASSOCIATION OF LESS FREQUENT SPECIES WITH HIGH OR LOW VALUES OF THE FACTORS

Species	Number of Occurrences	Factor				
		A	*B*	*C*	*D*	*E*
Acacia microcarpa F. Muell.	4	..	..	..	..	..
A. rigens A. Cunn.	5	..	..	−−	..	..
A. sclerophylla Lindl.	4	..	..	..	++	..
Aotus villosa Sm.	3	+	..	..	..	..
Atriplex stipitata Benth.	4	..	..	..	..	++
Baeckia behrii F. Muell.	4	++	..	..	..	..
Bassia parviflora Anders.	6	..	++	..	..	..
Beyeria opaca F. Muell.	5	+	..	+	..	..
Callitris verrucosa R. Br.	18	−−−	..	−−−	..	−
Cassia eremophila A. Cunn.	20	+++	..	..	++	+
Dianella revoluta R. Br.	3	+	..	..	..	..
Dodonaea stenozyga F. Muell.	6	..	..	..	..	..
Enchylaena tomentosa R. Br.	10	++	..	..	..	..
Grevillea huegelii Meiss.	19	..	..	..	..	..
Halgania cyanea Lindl.	3	..	..	−	..	..
Kochia pentatropis R. Tate	12	+	..	..	..	..
K. tomentosa (Moq.) F. Muell.	4	..	..	..	..	..
Lepidosperma viscidum R. Br.	7	−−	..	−−	..	−−
Lomandra leucocephala (R. Br.) Ewart	8	..	..	..	..	..
Melaleuca pubescens Schau.	8	−−−	..	..	..	..
Micromyrtus ciliatus J. M. Black	6	..	..	−−	..	..
Myoporum platycarpum R. Br.	5	..	..	..	..	..
Olearia muelleri Benth.	19	+++	..	..	−	..
Pittosporum phillyraeoides D.C.	4	++	..	++	−−	..
Santalum murrayanum F. Muell.	7	..	..	..	..	..
Stipa elegantissima Lab.	6	..	..	..	−−	..
S. mollis R. Br.	18	..	++	..	..	−
Trichinium seminudum J. M. Black	4	..	..	..	..	..
Vulpia myuros (L.) Gmel.	4	..	..	..	..	..

+++ or −−− indicates positive or negative association, with $P < 0.001$;
++ or −− indicates positive or negative association, with P : 0.001-0.01;
+ or − indicates positive or negative association, with P : 0.01-0.05.

The situation does not arise in the present data, but there is the possibility that, in a series of diagrams like those of Figure 3, one species might have a "hump" — perhaps a narrow one — in a unique position shared with no other species. In other words, the presence of that species in quantity would be diagnostic of a narrow range for the factor. This would not appear in the analysis, since no interspecific correlations would reflect it. Consequently the valuable information on the values of the factor which could be afforded by the presence of this species would go unused.

Another possible difficulty concerns the inclusion of data for the less common species. As is shown in Table 3, these species are often highly correlated with one or other factor, and may sometimes be diagnostic of a narrow range of one factor. But the extremely skew distributions, overloaded with zeros, which they show make one very diffident about including them. Consequently the precision which they might be able to add to the estimation of the factors for different sample areas is lost.

A point needing careful consideration is the relation between the sociological factors extracted in the course of factor analysis, and the environmental factors which play an important part in controlling the distribution of plants. They are not the same, though they may be closely related. The sociological factor is, in fact, simply an element in a description of the composition of the vegetation in a sample area. It relates to the *stand*, not the *biotope*. It may be interpreted as indicating something in common between the species of plants having similar coefficients — similarity in some particular feature of physiology, biology, or perhaps chorology; the value of the factor for a particular sample area may then be regarded as designating the extent to which this feature is represented in the plant population in that sample area. At times, the interpretation of the sociological factor may be closely related to some environmental factor — as, for instance, xerophytism, or salt tolerance; at others, the group of plants whose intercorrelations are responsible for a sociological factor may be a group of parasites and their common host, or a group of potential "nurse-plants" with the species needing their protection. Or, if the study covers a large area, it may be simply a group of species which, for historical reasons, have similar geographical distribution. But even where there is a close relation between the sociological factor and an environmental factor, it would be incorrect to equate the two. This would be equivalent to equating the dryness of a site with the xerophytism of the plants growing there, or the salinity of a site with the salt tolerance of its plant population — presumptive cause, that is, with presumptive effect. The effect may, used circumspectly, provide an excellent indication of the cause, but should be kept strictly distinguished from it.

It is not to be expected, however, that sociological factors — or even the distribution of individual species of plants — can be closely related to any single, simply measurable environmental factor. Whether or not a plant can grow successfully in a given position depends on the whole complex of factors occurring there, including their values at each successive stage of development; interactions (in the statistical sense) between these factors are often of great importance — for instance, rain in July may be favourable to the growth of annuals if there has been none in June, unfavourable otherwise. It is the high correlation between different environmental factors that often suggests a deceptively simple relationship between plant distribution and the environment. There is much to be said for the view that the complexes of environmental factors determining plant distribution can be indicated and measured better indirectly, through the plants themselves, than by direct physical measurements; this is, of course, the idea behind the use of "phytometers" in agricultural meteorology, and the attention devoted to phenology. If this is being done, factor analysis enables the whole vegetation to be used in the most appropriate way for the indication and indirect measurement of environmental complexes, once the complex of environmental factors on which a particular sociological factor depends has been approximately identified, and is bound to be a considerable improvement on the use of individual indicator species.

The population analysed, consisting as it did of groups of eight quadrats randomized within rectangular areas of 1.28 ha, gave no evidence of qualitative heterogeneity — there was no occasion to regard it as separable into two or more discrete communities. When the same factor analysis was applied to the individual quadrat data, however, it was clear that these quadrats fell in the main into two distinct classes; a minority of them contained intermediate quantities of the species mainly distinguishing these two classes, but also included several species missing from the two main classes. That the two classes should be apparent with individual quadrats and not with groups of quadrats presents no difficulty; the two classes occur on different parts of a catena, and the groups of quadrats were large enough, and extended in the right direction, to cover most or all of a catena — in other words, the two classes represent elements in a mosaic on a smaller scale than the areas on which the factor analysis was based. The proportions in which the elements of the small-scale mosaic are represented in the different rectangular areas vary sufficiently to provide a factor — and the most important factor — in the analysis, but the discrete variation in the mosaic has been smoothed out by combining quadrats.

It is difficult to decide what status to ascribe to the two discrete populations observed among the individual quadrat data. Are they to be regarded as separate plant communities or not? The commonsense view is that environmental conditions change continuously along a catena, and that in the absence of evidence of abrupt change the vegetational changes along it should also be treated as a continuum; the fact that the areas available to the ridge and valley vegetation are greater than those for the slope vegetation (leading to two clusters of points, and a thinner scatter in between) should not cause one to regard this continuum as two distinct communities with transitional zones. The plant-sociological purist, however, believing that variations in vegetation should be considered in the first instance independently of variations in environmental factors which might be responsible for them, might well prefer the latter view. At the moment there seems to be no criterion by which to decide between these views. If no clumping of points in the original variate-space, or the simpler derived factor-space, can be detected, one is entitled to rule out the possibility of discrete communities. But the converse does not hold so clearly, and the interpretation of such cases seems largely a matter of taste.

The extent to which factor analysis can be used in plant sociology will be severely limited by the heaviness of the computing work involved — at least until electronic computing facilities become more generally available. If the difficulties mentioned above could be overcome, there seems little doubt that it would be the most satisfactory technique for resolving and reducing to relative simplicity the complexities of plant distribution. But with ordinary computing methods it is bound to be very laborious, and is likely to be used in fundamental investigations into the structure of vegetation rather than in more descriptive work.

Even where not supported by clumping of points in factor-space, division of vegetation into arbitrary classes can well be justified for purposes of practical convenience, provided that its arbitrariness is recognized and that it is not claimed to represent an objective state of things. The most reasonable divisions would probably be obtained by making use of the factor analysis, separating the classes at convenient values (e.g. the means) of the factors. Very similar classifications to those resulting from such arbitrary division of the factor-space would probably be obtained by other methods based on interspecific correlation but not using factor analysis. It might be expected, for instance, that the associations of Braun-Blanquet and his school would represent particular regions of the factor-space which would be obtained if the vegetation on which they had been working were treated in this way, though substantial regions would be regarded as transitional, and left unallotted. Similarly, the classes separated by successive elimination of interspecific correlation (Goodall 1953*a*, 1953*b*) in the data used in the present paper might be expected to correspond fairly closely with regions in the factor-space described above.

Factor analysis does not result in a classification of vegetation in the ordinary sense, but in arrangement of the vegetational data in a multidimensional series. For such an arrangement, there appears to be no word in English which one can use as an antonym to "classification"; I would like to propose the term "ordination" (cf. Goodall 1954). In the present series of papers, the same data have now been subjected to objective procedures for both classification (Goodall 1953*a*) and ordination. But these two procedures by no means exhaust the possibilities of objective simplification of vegetational diversity. In subsequent investigations, it is intended to test other methods serving the same ends. In particular, it is hoped to bring forward further evidence bearing on the suitability of classification and ordination respectively as the basic approach in plant sociology. Until other possible methods have been tested, and data for other vegetation types analysed, it would be premature to attempt any comparative appraisal of the methods used so far.

IV. Acknowledgments

I am grateful to Professor A. S. Boughey, Professor J. S. Turner, and Dr. F. E. Binet for reading and criticizing this paper in draft. My very hearty thanks are also due to Dr. F. E. Binet for the great pains he took to explain to me the techniques of factor analysis.

V. References

Bartlett, M. S. (1950).—Tests of significance in factor analysis. *Brit. J. Psychol. Statist. Sect.* **3**: 77-85.

Goodall, D. W. (1952).—Quantitative aspects of plant distribution. *Biol. Rev.* **27**: 194-245.

Goodall, D. W. (1953*a*).—Objective methods for the classification of vegetation. I. The use of positive interspecific correlation. *Aust. J. Bot.* **1**: 39-63.

Goodall, D. W. (1953*b*).—Objective methods for the classification of vegetation. II. Fidelity and indicator value. *Aust. J. Bot.* **1**: 434-56.

Goodall, D. W. (1954).—Vegetational classification and vegetational continua. *Angew. PflSoziol., Wien.* Aichinger Festschrift (in press).

Holzinger, K. J., and Harman, H. H. (1941).—"Factor Analysis. A Synthesis of Factorial Methods". (University of Chicago Press: Chicago.)

Hotelling, H. (1933).—Analysis of a complex of statistical variables into principal components. *J. Educ. Psychol.* **24**: 417-41, 498-520.

Kulczynski, S. (1927).—Die Pflanzenassoziationen der Pieninen. *Bull. Int. Acad. Cracovie* (*Acad. Pol. Sci.*) 3B, Suppl. **2**: 57-203.

Sorensen, T. (1948).—A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Biol. Skr.* **5** (4): 1-34.

Spearman, C. (1927).—"The Abilities of Man: Their Nature and Measurement". (Macmillan: London.)

Tuomikoski, R. (1942).—Untersuchungen über die Untervegetation der Bruchmoore in Ostfinnland. I. Zur Methodik der pflanzensoziologischen Systematik. *Ann.* (*Bot.-Zool.*) *Soc. Zool.-Bot. Fenn. Vanamo* **17** (1): 1-203.

A QUANTITATIVE STUDY OF A PRESUMED HYBRID SWARM BETWEEN *EUCALYPTUS ELAEOPHORA* AND *E. GONIOCALYX*

By H. T. Clifford* and F. E. Binet†

(*Manuscript received March* 5, 1954)

Summary

From measurements of fruit lengths, fruit weights, and lengths of fruiting umbels of trees from the species *Eucalyptus elaeophora* and *E. goniocalyx* and their presumed hybrid swarm, a formula is calculated for taxonomic classification using statistical discriminant theory. The rates of misclassification expected with the use of this formula are estimated. A simple geometrical model of the relationship of the species and the hybrid is investigated.

I. Introduction

(*a*) *Preliminary Remarks*

In many localities in south-central Victoria there are stands of trees whose taxonomic position appears intermediate between *Eucalyptus elaeophora* F. Muell. and *E. goniocalyx* F. Muell. One of the authors (Clifford 1953, 1954) suggested previously that these intermediate trees are hybrids between *E. elaeophora* and *E. goniocalyx*. Although not yet confirmed by experiment, this relationship is assumed hereafter to save qualifying the terms "hybrid" and "parent" each time they occur.

The usual taxonomic classification of trees involves an unavoidable subjective element; although experience reduces the errors committed in this procedure, there is no easy method of assessing the extent of erroneous classification.

(*b*) *On Discriminant Functions*

In the statistical technique of discriminant analysis (Fisher 1936) we find a taxonomic tool almost entirely free from subjective impressions. By the use of the discriminant function, a tree is assignable to one of the two species or the swarm under consideration on the basis of numerical measurements alone. There is no doubt that misclassifications may occur in this process, but reliable estimates of the expected percentage rates of misclassification are easy to calculate.

Furthermore, a generalization of discriminant analysis (Fisher 1938) yields a geometrical picture of the interrelations of the species studied. A genetic model to account for these interrelations is under consideration.

Discriminant functions are linear combinations (that is, weighted sums and/or differences) of the numerical values of the measurements. In some cases, it might be convenient to use for these functions a scale

---

* Botany Department, University of Melbourne; present address: Botany Department, University of Durham.

† Department of Statistics, University of Melbourne.

different from the one in which the actual measurements were carried out (cf. Mather 1938); this is achieved by the use of certain functions (e.g. logarithms) of the measurements, rather than of the measurements themselves.

The coefficients in the linear combinations are chosen so as to maximize the ratio of the variance between the means of samples from different species to the variance within the samples. In other words the weights (which may be positive or negative) are adjusted so that interspecies differences are emphasized at the expense of intraspecies, individual differences.

This paper describes such an analysis of the measurements of properties made upon samples from each of 50 trees from a hybrid swarm and the same number of each of the parental species.

(*c*) *Collection of Material*

The parental species were sampled only in localities where interbreeding with the other parent or with a hybrid swarm could be reasonably excluded; in areas with a low rainfall gradient no collections were made unless the nearest hybrid or second parent was several miles away; in areas with steep rainfall gradient this minimum distance was reduced to 2 miles. These localities spread from the Southern Flinders Range, the Mount Lofty Range, and the Grampians Range through the Eastern Highlands as far north as Canberra for *E. elaeophora;* and from the Grampians Range along the Eastern Highlands to Mt. Wilson (N.S.W.) for *E. goniocalyx.*

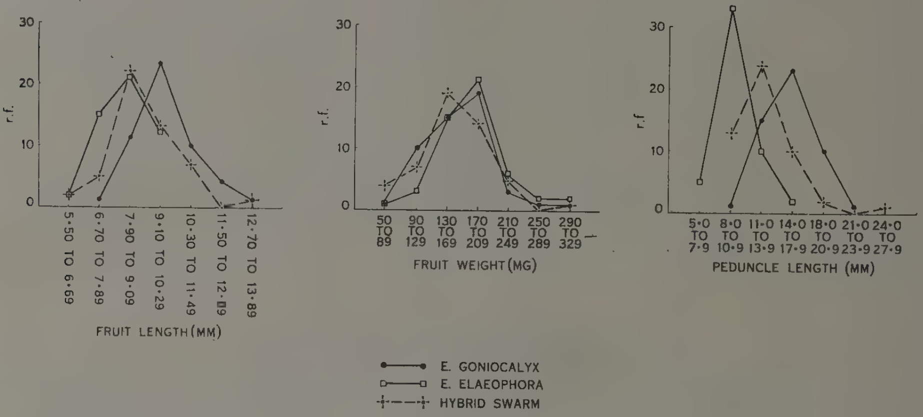


Fig. 1.—Frequency polygons for fruit length, fruit weight, and peduncle length in the three samples.

The hybrid swarm sampled was in a forest on a hillside between Upper Ferntree Gully and Tremont (two townships in the Dandenong Range about 20 miles east of Melbourne). In this forest samples were collected from the first 50 accessible trees apparently belonging to the group

E. elaeophora-E. goniocalyx. No difficulty was encountered in deciding whether a tree belonged to this group or not, because all the other *Eucalyptus* species present were very different from those being studied. (They were *E. radiata*, *E. obliqua*, *E. viminalis*, and *E. macrorrhyncha.*)

Table 1

SAMPLE MEANS AND VARIANCES

		E. elaeophora	Hybrid Swarm	*E. goniocalyx*
Fruit weight (mg)	Mean	186.02	159.78	166.20
	Variance	2090.9	2080.91	2097.31
Fruit length (mm)	Mean	8.226	8.928	9.920
	Variance	0.8665	1.616	1.413
Peduncle length (mm)	Mean	10.058	13.012	15.864
	Variance	3.685	9.529	6.963

From each of the 150 trees sampled, 10 fruits were taken at random and their weights and lengths measured. A similar procedure was adopted for peduncle lengths of fruiting umbels. These organs were chosen because they were mature and growth in them had ceased. The weight of each fruit as well as its length was measured because, for a given length, weight was very dependent on shape, and this had been shown to be characteristically different in the two species.

II. Statistical Analysis

(a) *Processing the Measurements*

The measurements are presented as frequency polygons in Figure 1, from which it can be seen that for each set of measurements the values for the parents and the hybrids overlap considerably. If, however, the characters are considered in pairs and their measurements plotted in two-dimensional scatter diagrams, it can be seen from Figure 2 that any of the three pairs divides the parents reasonably sharply. The hybrids

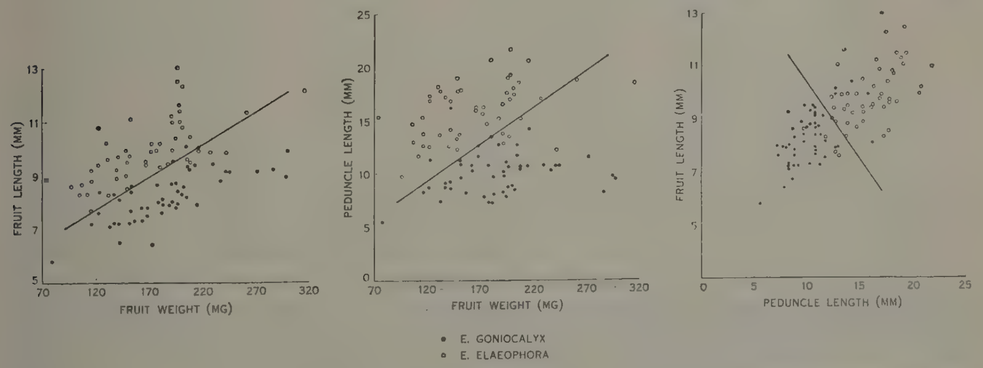


Fig. 2.—Scatter diagrams for the three pairs formed from three measurements in the parental samples.

were omitted here as they would have obscured the dividing line between the parental species. The straight lines were drawn by eye and represent crude approximations to standard linear discriminant functions.

TABLE 2

TRANSFORMED SAMPLE MEANS

	W	L	P
E. elaeophora	122.10	91.20	99.78
Hybrid swarm	115.74	96.62	113.34
E. goniocalyx	117.42	99.36	125.50

The first step towards statistical analysis was the computation of the sample means and variances of the original measurements. These are shown in Table 1.

The measurements were transformed so as to satisfy approximately an assumption underlying the standard technique of discriminant analysis, namely equality of population variances. The transformations follow:

$$W = 10 \times (\text{fruit weight in mg})^{\frac{1}{3}}$$
$$L = 100 \times \log_{10}(\text{fruit length in mm})$$
$$P = 10 \times (\text{peduncle length in mm})^{\frac{1}{2}}.$$

Tests on the transformed measurements showed no evidence of non-normality.

TABLE 3

TRANSFORMED SAMPLE VARIANCES AND COVARIANCES

		W	L	P
E. elaeophora	W	103.68	37.45	27.90
	L	37.45	24.73	25.47
	P	27.90	25.47	91.27
Hybrid swarm	W	138.11	57.18	75.11
	L	57.18	37.26	49.66
	P	75.11	49.66	167.49
E. goniocalyx	W	117.72	37.78	49.26
	L	37.78	25.95	29.04
	P	49.26	29.04	112.91

Tables 2 and 3 summarize the means, variances, and covariances of the transformed measurements. These tables contain all the information needed for discriminant analysis.

(*b*) *Comparison of the Populations*

(i) *Comparison of Variances.*—The corresponding sample variances for the parental species and the hybrid swarm were compared by means of the F-test. The differences between the parental species were not significant at the upper $2\frac{1}{2}$ per cent. point (corresponding to a 5 per cent. two-tailed level), thus indicating that the transformations set out in the section above were successful. The appropriate parental sample variances were pooled and compared with the corresponding sample variances in the hybrid swarm (see Table 4). All the characters appear more variable in the hybrids than in the samples from the parental species, but only for P is this difference significant.

TABLE 4

COMPARISON OF SAMPLE VARIANCES

	W	L	P
Parents pooled	110.70	25.34	102.09
Hybrid swarm	138.11	37.26	167.49
Ratio H.S./P.P.	1.248	1.470	1.641*

* Significant at the 5 per cent. level.

(ii) *Comparison of Correlations.*—Using Fisher's method (see e.g. Snedecor 1946, p. 151) the corresponding correlation coefficients in the samples from the parental species and in the sample from the hybrid swarm were compared. All three correlation coefficients in the hybrid sample were larger than the corresponding parental ones, but none significantly (Table 5).

TABLE 5

SAMPLE CORRELATIONS

	W and L	W and P	L and P
E. elaeophora	0.739	0.287	0.536
Hybrid swarm	0.797	0.494	0.629
E. goniocalyx	0.684	0.427	0.537
Pooled, within parent species	0.710	0.363	0.536
Pooled, within all three groups	0.745	0.417	0.576

(iii) *Comparison of Dispersions.*—The tests described in the above two sections do not supply evidence for discrepancy between the correlation structures of the three populations. Nevertheless a trend seems to appear pointing towards larger variances and covariances in the hybrid swarm than in the parental species. As the tests indicating this trend are not independent, their results cannot be pooled. However, a blanket-test exists to reveal overall differences between correlation structures; this test consists of the comparisons of the determinants of the dispersion matrices (Box 1949). This test appears particularly appropriate to our data as all the apparent discrepancies are of a comparable order and in the same direction.

Two tests were carried out: (1) comparison of the three determinants; (2) comparison of the determinant of the pooled parental sample dispersion matrix with that of the sample from the hybrid swarm. Neither test turned out to be significant.

(iv) *Comparison of Means.*—A study of the variances, correlations, and dispersions within the three samples revealed no evidence in favour of any discrepancy between the populations. It may be, however, that there are differences between the mean vectors of the three populations.* To investigate this we now postulate that the three dispersion matrices are identical in the populations and then proceed to apply the test devised by Wilks (1932).

The statistic serving as appropriate criterion is

$$\Lambda = \frac{|\, W \,|}{|\, B + W \,|}, \qquad \dots\dots\dots\dots\dots\dots \quad (1)$$

where W is the pooled matrix of sums of squares and products within all the samples, around the individual sample centroids, and B is the matrix of sums of squares and products between the samples, around the centroid of all observations.

For the present data $\Lambda = 0.3456$. The significance of this value is tested by referring

$$F = \frac{1 - \sqrt{\Lambda}}{\sqrt{\Lambda}} \cdot \frac{146}{3} = 34.12$$

to the F tables with 6 and 292 degrees of freedom (Rao 1952, pp. 260, 345). This turns out to be significant at the 0.1 per cent. level. We conclude that the mean vectors of the populations are fundamentally different.

(c) *Internal Analysis*

Assuming trivariate normal distribution of W, L, and P, a common dispersion matrix, and different mean vectors in the three populations, we can visualize a three-dimensional space, with three probability masses representing the three populations (two parental species and one hybrid). Within each of these masses the surfaces of equal probability are concentric, similar, and similarly situated ellipsoids; the centroids of the three masses are different. The three systems of concentric ellipsoids are similar and similarly situated, and the dimensions of the corresponding ellipsoids of the three systems are the same.

The parameters specifying this system are reliably estimated by the appropriate statistics calculated from samples of 50 individuals each. The arrangement of the centroids will be considered in the next section.

The internal structure of the masses is described by the lengths and directions of the principal axes of the ellipsoids. These were estimated

---

* We represent the situation by a three-dimensional space in which the centroids of the samples are points having as coordinates the sample means of W, L, and P. The assumption underlying the test employed is that all displacements between these three points are due to chance alone, i.e. that the three samples are random samples from the same multivariate population. The test, when yielding a significantly small critical value, refutes this assumption.

(following Pearson 1901) by calculating the latent roots and latent vectors of the pooled correlation matrix, i.e. of the matrix formed by the last row of Table 5, with units in the diagonal. The latent roots and latent vectors of this matrix are given in Table 6.

The latent vectors represent the directions of the principal axes in the w, l, p coordinate system, obtained on dividing the original variates W, L, P by their estimated standard deviations. The elements of these vectors are the cosines of the angles between the principal axis and the appropriate coordinate axis. The square roots of the latent roots estimate the half-lengths of the principal axes of the iso-probability surface whose distance from the centroid is unity when measured along any of the three original axes.

Tests of significance devised by Bartlett (1950, 1951) showed that the above values of the latent roots can be accepted as evidence that in the population (1) the ellipsoids are eccentric, i.e. they are not spheres; and (2) the length of the second largest principal axis is not zero, i.e. the ellipsoids do not degenerate into lines.

TABLE 6

LATENT ROOTS AND VECTORS OF THE SAMPLE DISPERSION MATRIX

Roots	w	l	p
2.169	0.583	0.627	0.517
0.604	—0.545	—0.170	0.821
0.227	0.602	—0.761	0.243

No significance tests exist to show that the length of the third principal axis is not zero, i.e. that the ellipsoids do not in fact degenerate into ellipses. We accept the non-zero estimate merely to render the visual image more suggestive.

(*d*) *Arrangement of Population Centroids*

(i) *Collinearity.*—The sample centroids were found to be non-collinear. If the population centroids are collinear, then the population value of the second latent root of the matrix $W^{-1}B$ is zero (Fisher 1938). If the sample value of the first latent root of this matrix is highly significantly large and the population value of the second root is zero, then the quantity

$$n \log_e (1 + a),$$

(where n is one less than the total number of individuals and a is the sample value of the second latent root) is distributed approximately as χ^2 with three degrees of freedom (Marriott 1952).

We obtain the following three roots, 1.145, 0.024, 0.000, the first of which is highly significantly large. Hence to test whether the non-collinearity of the sample centroids is compatible with an assumption of collinear population centroids we calculate

$$149 \log_e (1 + 0.024) = 3.55,$$

which is not significant, so that the assumption of collinearity is justified.

(ii) *Symmetry.*—The sample centroid of the hybrid swarm was slightly nearer to the centroid of *E. goniocalyx* than to that of *E. elaeophora*. To test for symmetry of the population centroids, a simple generalization of Wilks's test (see Rao 1952, p. 270) is applied.

The statistic used as criterion is

$$\Lambda' = \frac{| W |}{| W + B' |}, \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

where B' is the matrix of the sums of squares and products due to asymmetry between the sample centroids. The significance of Λ' is tested by referring

$$F = \frac{1 - \Lambda'}{\Lambda'} \cdot \frac{147}{3}$$

to the F tables with 3 and 147 degrees of freedom.

Here $\Lambda' = 0.955$, $F = 2.33$, which is not significant. Hence we find no evidence that the arrangement of the population centroids is other than symmetrical.

(*e*) *Taxonomy*

The appropriate tests of significance showed that omission of any one of the three variates decreases significantly the separation of the sample centroids (Rao 1952, p. 252). Hence classification should be based on all the three variates.

As the population centroids are assumed collinear, a single discriminant function is all that is required. This function is a linear combination of W, L, and P, with coefficients proportional to the elements of the latent column vector which belongs to the largest latent root of the matrix $W^{-1} B$. The function obtained from the present data is

$$- 0.9702W + 0.16117L + 0.05775P. \quad \ldots\ldots\ldots \quad (3)$$

The coefficients of this function are adjusted so that its estimated variance is unity. On rewriting in terms of the original measurements it becomes

$$\begin{aligned} &- 0.9702 \times (\text{fruit weight in mg})^{\frac{1}{3}} \\ &+ 16.117 \times \log_{10} (\text{fruit length in mm}) \\ &+ 0.5775 \times (\text{peduncle length in mm})^{\frac{1}{2}}. \quad \ldots\ldots\ldots \quad (4) \end{aligned}$$

The mean values of this discriminant function in the three samples are shown in Table 7.

When applying the discriminant function to classify an individual tree, that tree is assigned to the population whose mean is nearest to the value calculated by substituting into the discriminant function (4) the average of the measurements taken on that tree. Accepting the sample means as the best estimates of the population means, a rule of classification is obtained. This rule is shown in Table 8.

TABLE 7

MEANS OF DISCRIMINANT FUNCTION

Population	Sample Mean of Discriminant Function
E. elaeophora	8.616
Hybrid swarm	10.567
E. goniocalyx	11.870

TABLE 8

CLASSIFICATION RULE BASED ON SAMPLE MEANS ONLY

Observed Value of Discriminant Function	Classification of Individual
$\leqslant 9.591$	*E. elaeophora*
9.592 — 11.217	Hybrid
$\geqslant 11.218$	*E. goniocalyx*

If we assume, on genetical grounds, that the centroid of the hybrid population is midway between the centroids of the parental populations, then we get an alternative rule of classification (Table 9). The two rules lead to different decisions only over two short intervals; in both intervals the classification is rather unreliable.

TABLE 9

CLASSIFICATION RULE BASED ON SAMPLE MEANS UNDER ASSUMPTION OF SYMMETRY

Observed Value of Discriminant Function	Classification of Individual
$\leqslant 9.428$	*E. elaeophora*
9.429 — 11.056	Hybrid
$\geqslant 11.057$	*E. goniocalyx*

Whichever of these two rules is used, misclassifications will almost always occur because the populations overlap. The expected percentage rate of misclassification is a measure of the reliability of the method. This rate is estimated by a method due to Wilks (1943, p. 144). These estimates are given in Table 10.

It can be seen that even when a combination of three measurements is used, the hybrids overlap considerably with the parents, especially with *E. goniocalyx*. The two parental species, however, separate well. This is shown in Figure 3, which may be compared with Figure 1.

In considering the overlap of the hybrid and parental populations it should be remembered that the sample presumed as coming from the hybrid swarm included all accessible trees in the stand studied, and so would have included trees from the parental species had these been present. Although no such individuals were observed, if they nevertheless occurred in the sample, then the estimated expected percentage rates of misclassification would understate the taxonomic value of the linear discriminant function.

TABLE 10

ESTIMATED EXPECTED PERCENTAGE RATES OF MISCLASSIFICATION

Tree Species	Tree Misclassified as	Rate, when Using Rule in Table 8	Rate, when Using Rule in Table 9
E. goniocalyx	Hybrid	25.8	21.2
E. goniocalyx	*E. elaeophora*	1.2	0.8
Hybrid	*E. elaeophora*	16.5	21.2
Hybrid	*E. goniocalyx*	25.8	21.2
E. elaeophora	Hybrid	16.5	21.2
E. elaeophora	*E. goniocalyx*	0.5	0.8

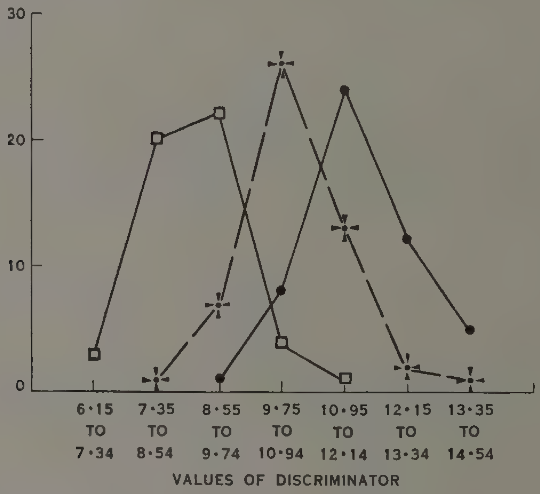


Fig. 3.—Frequency polygon for the discriminator in the three samples. Legend as in Figure 1.

III. CONCLUSION

It has been demonstrated that the data are consistent with the hypothesis that the tree populations are each trivariate normal with identical dispersion matrices, and with collinear and equally spaced centroids. Each centroid is the centre of a probability mass and the loci of equal probabilities are similar and similarly situated ellipsoids.

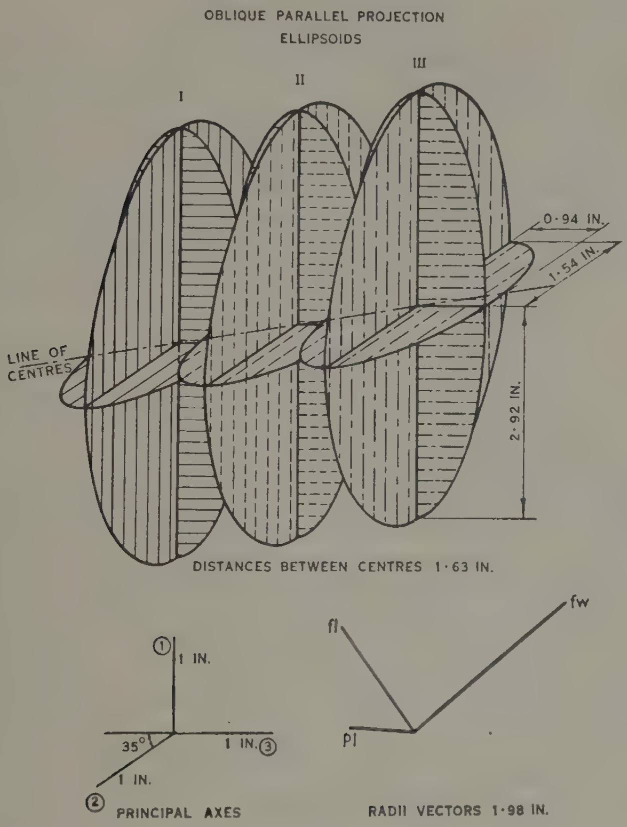

OBLIQUE PARALLEL PROJECTION
ELLIPSOIDS
I
II
III
LINE OF CENTRES
0·94 IN.
1·54 IN.
2·92 IN.
DISTANCES BETWEEN CENTRES 1·63 IN.
①
1 IN.
35°
1 IN. ③
1 IN.
②
PRINCIPAL AXES
fl
fw
pl
RADII VECTORS 1·98 IN.

Fig. 4.—Isoprobability surfaces.

To obtain a simple illustration of the geometrical relationship between the three populations, the estimated dimensions of these ellipsoids for one selected probability, namely 1.992×10^{-4}, were calculated. A diagram of these ellipsoids is shown in Figure 4*. The axial lengths are 95 per cent. (two-sided) tolerance limits. Each ellipsoid contains 72 per cent. of the total probability mass in each instance.

The angles between the three principal axes and the line connecting the centres are 81°, 51°, and 139°. The direction of this line corresponds to the vector on which the taxonomic discriminant function is based.

Figure 4 does not add anything to the statistical analysis, all the relevant information being contained in Tables 2-10. The diagram is merely intended as a pictorial representation of the overlap of the three populations and of the orientation of axes determining the internal structure of the three probability masses in relation to the arrangement of the centroids.

---

* The symbols *fw*, *fl*, and *pl* denote the variates *w*, *l*, and *p*, as defined in the text. One in., according to the scale adopted, represents one unit of a variate.

IV. ACKNOWLEDGMENTS

Our thanks are expressed to Professor J. S. Turner, for suggesting the problem, to Associate Professor M. H. Belz, for assistance in preparation of the paper, to Mr. D. Ashton, Mr. J. Robbins, Mr. A. Gregson, Mr. T. Arthur, Mr. K. Harrop, Mr. A. Hoyd, Mr. B. Davidson, Mr. C. D. Boomsma, Mr. R. Specht, Miss C. Eardley, and Miss K. Pike, for assistance in collecting the material, to Mr. W. M. Holmes, for preparing the diagram, and to Miss A. G. Doig, for assistance in the computations.

V. REFERENCES

BARTLETT, M. S. (1941).—The statistical significance of canonical correlations. *Biometrika* 32: 29.

BARTLETT, M. S. (1950).—Tests of significance in factor analysis. *Brit. J. Psychol. Statist. Sect.* 3: 77.

BARTLETT, M. S. (1951).—A further note on tests of significance in factor analysis. *Brit. J. Psychol. Statist. Sect.* 4: 1.

BOX, G. E. P. (1949).—A general distribution theory for a class of likelihood criteria. *Biometrika* 36: 334.

CLIFFORD, H. T. (1953).—On the distribution of the species of *Eucalyptus* in the region of the Dandenong Range, Victoria. *Proc. Roy. Soc. Vict.* 65: 30.

CLIFFORD, H. T. (1954).—A method of analysing hybrid swarms with special reference to two *Eucalyptus* species. *Heredity* 8 (in press).

FISHER, R. A. (1936).—The use of multiple measurements in taxonomic problems. *Ann. Eugen., Lond.* 7: 179.

FISHER, R. A. (1938).—The statistical utilization of multiple measurements. *Ann. Eugen., Lond.* 8: 376.

MARRIOTT, F. H. C. (1952).—Tests of significance in canonical analysis. *Biometrika* 39: 58.

MATHER, K. (1938).—"Biometrical Genetics." Ch. 3. (Methuen and Co. Ltd.: London.)

PEARSON, K. (1901).—The lines of closest fit to a system of points. *Phil. Mag.* 2: 559.

RAO, C. R. (1952).—"Advanced Statistical Methods in Biometric Research." (John Wiley & Sons Inc.: New York.)

SNEDECOR, G. W. (1946).—"Statistical Methods." 4th Ed. (State Collegiate Press: Ames, Iowa.)

WILKS, S. S. (1932).—Certain generalizations in the analysis of variance. *Biometrika* 24: 471.

WILKS, S. S. (1943).—"Mathematical Statistics." (Princeton University Press.)

AUSTRALIAN SPECIES OF *SARGASSUM*, SUBGENUS *PHYLLOTRICHIA*

By H. B. S. WOMERSLEY*

(*Manuscript received March* 16, 1954)

Summary

A revision of the Australian species of the subgenus *Phyllotrichia* of *Sargassum*, based on field knowledge of most species, abundant herbarium material, and a study of the type specimens in English, European, and Australian herbaria, results in the recognition of eight species. Specific variation, seasonal development, and the relationship of *Phyllotrichia* to the other subgenera of *Sargassum* are discussed.

INTRODUCTION

Phyllotrichia is largely a typically Australian section of *Sargassum*. Of the 10 species which may now be recognized, eight are Australian, with five found in the temperate waters of southern Australia, two around tropical Australia, and one so far known only from Lord Howe I. Two species are known from outside Australasia, one from the Canary Is. and one from Japan. These 10 species should probably be increased to 12 by the union of the subgenus *Schizophycus* with *Phyllotrichia* (see below).

Present-day knowledge of the species of *Sargassum* is still very largely dependent on J. G. Agardh's monograph (1889), which established five subgenera. Since then the only major works published are those of Grunow (1915, 1916), and Setchell (1931, 1933, 1935, 1936). Since Setchell summarized the taxonomic history of the genus and has given the best account of it of recent years, it is unnecessary to review the genus here.

Collections and ecological surveys on the southern Australian coast during the last 10 years have indicated the most unsatisfactory state of knowledge of *Sargassum*, and during 1952 the types† of Australian species in overseas herbaria were studied, notably those at Kew and the British Museum (Natural History) in England, at Lund in Sweden, and at Paris in France. This paper deals with only one section of *Sargassum*. It is proposed to deal with the subgenus *Arthrophycus* and the southern Australian species of *Eusargassum* at a later date.

In view of the fundamental importance of J. G. Agardh's monograph, the specimens in the Agardh Herbarium in Lund are of great importance. It is rather disturbing, therefore, to find the specimens rather less impressive than his descriptions and figures. Frequently the representation of a species is not good, and in *Arthrophycus* the basal and upper parts of a plant associated on one sheet or in one folder are sometimes not united, thus giving rise to doubts whether they are the same species. In some instances also it is clear that J. G. Agardh did not have type material of previous authors, and his concepts are not always correct. Most subsequent authors have followed his concepts.

---

* Department of Botany, University of Adelaide.

† Photographs of the type specimens of the species of *Phyllotrichia* are deposited in the Algal Herbarium, University of Adelaide.

While J. G. Agardh's monograph of *Sargassum* is still the basis of our understanding of this difficult genus, and was in its time an outstanding account of the species and their relationships, it is clear that most of the species and groups need critical revision on the basis of wide field knowledge of developmental stages and ecological variations, together with a study of the type specimens.

Grunow's studies (1915, 1916) were published after his death and provide the only survey of the whole genus since that of J. G. Agardh. In general he followed J. G. Agardh's classification, and while he described relatively few new species, his varieties and forms are numerous. Fortunately perhaps, he described only a few varieties of the species of *Phyllotrichia*, and although his specimens have not been seen by the present author, it is abundantly clear that these varieties are mere developmental or ecological forms, quite unworthy of recognition. The same criticism probably applies to his work on the other subgenera of *Sargassum*.

Lucas (1935) described a new species from Lord Howe I., but in his account of the South Australian species (1936) he followed J. G. Agardh's classification and concepts, contributing nothing new.

The account of the seasonal development of the southern Australian species given below shows the necessity for collections of fully developed and fertile specimens.* Frequently it is necessary to study a species at all seasons of the year.

In the account of the species detailed locality data have not been given, owing to its large bulk and doubtful value. All specimens in Brisbane (Botanic Gardens Herbarium and University), Sydney (Botanic Gardens), Melbourne (National Herbarium and University), Tasmania (University and Launceston Museum), Adelaide (University), and Perth (University and State Herbarium) have been examined and annotation labels placed on the sheets. The distribution of each species is summarized below from all the above records and from reliable literature records.

PHYLLOTRICHIA AND ITS RELATION TO THE OTHER SUBGENERA

Phyllotrichia was defined by J. G. Agardh (1889) (see also Setchell 1931, p. 244) as having primary branches emerging from the stem or main axis as "foliar expansions", which are pinnatifid and usually flattened below, but may become cylindrical above where they bear vesicles and receptacles. The vesicles were regarded as being essentially without any terminal outgrowth (i.e. mutic).

---

* The same comment applies equally to species of *Arthrophycus*.

J. G. Agardh's second subgenus, *Schizophycus,* has similar, though more subdivided, pinnate foliar expansions arising from the stems, but the vesicles were regarded as developing from the lower portion of a leaf or leaf segment, thus being crowned with a simple or branched prolongation.

The other subgenera (*Bactrophycus, Arthrophycus,* and *Eusargassum*) differ from *Phyllotrichia* and *Schizophycus* in having only distinctly differentiated and essentially simple (very rarely branched) leaves.

Apart from the Australian species of *Phyllotrichia,* J. G. Agardh (1889, p. 55) recognized two other species, *S. piluliferum* (Turner) C. Agardh from Japan and *S. desfontainesii* (Turner) C. Agardh from the Canary Is. Though Setchell (1931, p. 244) queried whether these should be placed under *Phyllotrichia,* Turner's figures (1808, Plate 65; 1811, Plate 190, respectively) and Setchell's photograph (1933, Plate 4) of the type of *S. piluliferum* indicate that they probably come within this subgenus, since the branches bear pinnately branched laterals and the vesicles are mutic.

The two distinctions of Agardh (followed by Setchell) between *Phyllotrichia* and *Schizophycus* lie in the greater degree of branching and development of the laterals, and in the possession of a terminal leaflet on the vesicles in the latter. The range of form of the species of *Phyllotrichia* described below shows, however, that neither of these differences is satisfactory. The degree of branching of the laterals varies considerably in several species, such as *S. varians,* and is largely dependent on the age of the plant. Presence or absence of prolongations on the vesicles is a variable character in *S. varians* (where such prolongations are usually absent but may reach 2 cm long and 2 mm broad) and also in *S. verruculosum,* where the slender mucro may reach over 1 cm long and bear cryptostomata; in *S. decurrens* the vesicles are normally mutic but may have a slender mucro up to 1 cm long; in *S. heteromorphum, S. sonderi,* and *S. decipiens* there is normally a small, pointed mucro; while in *S. peronii* and *S. howeanum* the vesicles are probably always mutic.

J. G. Agardh's and Setchell's (1933, p. 34) belief that the vesicles in *Phyllotrichia* are always mutic is clearly wrong, and the distinction between *Phyllotrichia* and *Schizophycus* is rendered more doubtful by Setchell's (1933, pp. 34-6) account of the species of *Schizophycus.* In *S. patens* he recognized three varieties; var. *typicum* has "vesicles prolonged into an appendage which is still phyllode-like, in that it is usually divided"; var. *rodgersianum* has "the projection at the tip of the bladder reduced to almost a point (or mucro) or at least simple and undivided"; var. *schizophylla* is intermediate between these two.

It seems clear that these two subgenera cannot be maintained on vesicle or branching characters, and the species of *Schizophycus* can best be placed under *Phyllotrichia.* The vesicles in the different species form a graded series from completely mutic ones to those with branched terminal prolongations (*S. patens* var. *typicum*).

Phyllotrichia (including *Schizophycus*) is then readily recognized by the branched character of the laterals on the main branches, i.e. the presence of "foliar pinnatifid expansions", as distinct from the individual, simple "leaves" of *Bactrophycus, Arthrophycus,* and *Eusargassum.* In a few species only of these latter groups are occasional branched leaves found. The only species of *Phyllotrichia* which may not be readily recognized is *S. decipiens,* which has crowded, slender, leaf-like appendages on all sides of the lower part of the main branches. These may be simple but are frequently branched once to several times, especially in mature plants.

Within *Phyllotrichia* J. G. Agardh distinguished five tribes. The differences between them are not well defined or important, and they will not be recognized here.

Besides the Australasian species, the following species may be included under *Phyllotrichia*:

S. piluliferum (Turner) C. Agardh, from Japan,
S. desfontainesii (Turner) C. Agardh, from the Canary Is.,
S. pinnatifidum Harvey, from Japan and Hong Kong,
S. patens C. Agardh, from Japan and Hong Kong,

and possibly

S. tosatense Yendo from Japan.

Setchell (1933) should be consulted for descriptions of the Japanese species.

SEASONAL DEVELOPMENT AND VARIATION OF THE SPECIES OF PHYLLOTRICHIA

Much of the duplication of species within *Phyllotrichia* has been due to a lack of understanding of the development of the species, which is perhaps to be expected when only herbarium specimens — and often only poor ones — are available.

The following general account applies to the southern Australian species, several of which have been studied in the field throughout the year. The development of the tropical species (*S. peronii* and *S. decurrens*) is probably very similar.

From the basal holdfast, which is usually conical and solid, arise one to a few stout stems, which may be compressed or terete, and vary from only about 1 cm in length up to 20 cm. From the stem apex arise usually two to several main branches which are well described as "pinnatifid foliar expansions", i.e. deeply divided, flattened, narrow to broad "phylloids" (e.g. Plate 3, Fig. 1), consisting of the main branch axis with laterals which may be simple or subdivided. The main branches are strongly distichous in some species (*S. peronii,* Plate 1, Fig. 2, and *S.*

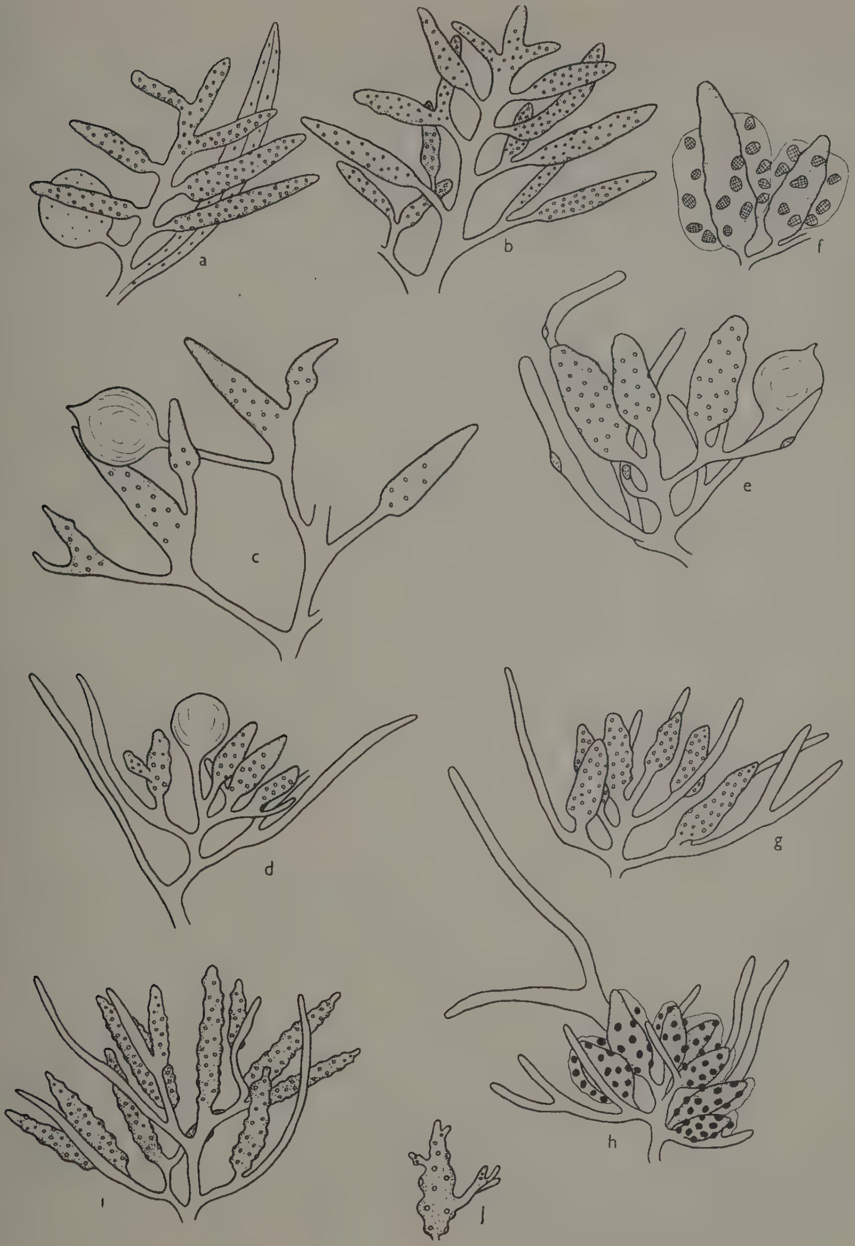


Fig. 1.—*a*, *S. peronii*: a group of young receptacles with a ramulus and vesicle. *b*, *S. peronii*: an older and more branched group of receptacles. *c*, *S. heteromorphum*: receptacles and vesicle. *d*, *S. sonderi*: receptacles and vesicle subtended by filiform ramuli. *e*, *S. decipiens*: receptacles of a male plant. *f*, *S. decipiens*: two receptacles of a female plant with developing zygotes held in the surrounding mucilage. *g*, *S. varians*: receptacles of a male plant. *h*, *S. varians*: receptacles of a female plant with developing zygotes. *i*, *S. verruculosum*: a group of mature receptacles. *j*, *S. verruculosum*: a single receptacle showing branching.

decurrens, Plate 2, Fig. 1), less so in others. In *S. decipiens* (Plate 4, Fig. 1) the axis of the main branches bears simple or branched narrow laterals ("leaves") on all sides.

The main branches are lost each year, and new ones arise from the apex of the stem. At certain times of the year (February to June in most species) only this basal part of the branches will be present. In winter (June onwards), however, growth of the ends of the main branches continues, forming much narrower (often terete and filiform) divisions than in the basal part. On these filiform upper ramuli the vesicles and receptacles develop, usually from July onwards. In early summer (November to January), depending on local rough weather, the fertile main branches are completely lost, leaving only scars on the stems.

In some species (*S. decipiens, S. sonderi, S. heteromorphum*) the vesicles are only formed on the upper ramuli, usually before receptacles are developed. In others (*S. peronii, S. decurrens, S. varians,* and *S. verruculosum*) they may be present on the basal parts, but are found in greater numbers when fertile fronds develop.

The receptacles are usually formed in racemose groups on, or subtended by, the upper ramuli (Fig. 1). They are formed by ramuli becoming swollen and developing conceptacles. At first they are short and bluntly pointed, but as they develop they elongate considerably. Whether the receptacles are petiolate or not depends largely on the state of development. Individual receptacles may branch furcately or, in some species, produce small outgrowths which may develop into small receptacles (e.g. *S. verruculosum,* Fig. 1*j*).

Variation within any particular species therefore depends largely on the season. Some rock pool forms, or plants growing in very rough habitats, appear to retain the juvenile form in which basal parts only occur (e.g. *S. heteromorphum,* Plate 2, Fig. 2, right-hand specimen; *S. sonderi,* Plate 3, Fig. 1).

The Australian species of *Phyllotrichia* are apparently normally dioecious. Differences in size between male and female receptacles may occur, but are usually only slight. The eggs are extruded in mucilage from the conceptacles before fertilization, and the zygotes (at least in *S. decipiens* and *S. varians*) develop to a many-celled stage held in the mucilage (Fig. 1*f*, *h*), without apparently reaching the rhizoid stage before liberation from the mucilage.

KEY TO AUSTRALIAN SPECIES OF THE SUBGENUS PHYLLOTRICHIA

1. Whole of mature main branches distichous, branch axes flat and winged, 5-10 mm broad, tapering evenly 2

Mature main branches not completely distichous (though the basal part may be), branch axes terete or flattened but usually under 4 mm broad (lower segments of *S. heteromorphum* may be up to 1 cm broad) 3

2(1). Laterals of main branches tapering fairly evenly from the axis to narrow acute apices, always branched .. .. *S. decurrens*
Laterals of main branches more leaf-like, constricted at the base and mostly simple .. .. *S. peronii*

3(1). Main branch axes terete-angular, vesicles small (1-3 mm dia.), lower laterals not retrofract 4
Main branch axes compressed below, lower laterals retrofract, vesicles large (4-10 mm dia.) 7

4(3). Lower parts of main branches very distinct from upper, lower segments 5-10 mm broad .. .. *S. heteromorphum*
Lower parts of main branches grading into upper, lower segments narrow (up to 1-5 mm broad) 5

5(4). Lower laterals of main branches narrow, simple, or branched, not or only slightly differentiated 6
Lower laterals of main branches distinct, often large and deeply pinnate (segments 2-5 mm broad) .. .. *S. sonderi*

6(5). Stem compressed, lower laterals only slightly broader than upper .. *S. decipiens*
Stem terete, lower laterals not differentiated .. .. *S. howeanum*

7(3). Stem compressed, mature lower laterals markedly retrofract from the flattened axes of the main branches .. .. *S. varians*
Stems terete, lower laterals retrofract and old branch axes usually flexuose .. .. *S. verruculosum*

Sargassum decurrens (R. Brown in Turner) C. Agardh, Sp. Algarum **1:** 42 (1821); Syst. Algarum 308 (1824); J. Agardh, Sp. Gen. Ordines Algarum **1:** 285 (1848); Acta Univ. Lund. **9:** 53 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 47, pl. 15, fig. 2 (1889); De Toni, Sylloge Algarum **3:** 13 (1895); Grunow, Verh. zool.-bot. Ges. Wien **66:** 334 (1915); Harvey, Phycol. Aust. 3: pl. 145 (1860); Sonder, Alg. trop. Aust. 7 (1871)

Plate 2, Fig. 1

Fucus decurrens R. Brown in Turner, Fuci Plant. Gen. Bot. **3:** pl. 194 (1811).

Pterocaulon decurrens Kützing, Phycol. General. 360 (1843); Sp. Algarum 606 (1849); Tab. Phycol. **10:** pl. 65 (1860).

Sargassum scabripes J. Agardh, Acta Univ. Lund. **9:** 52 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 48, pl. 2 (1889); De Toni, Sylloge Algarum **3:** 14 (1895); Grunow, Verh. zool.-bot. Ges. Wien **66:** 335 (1915); May, Contrib. N.S.W. Nat. Herb. **2:** 50 (1953).

Holdfast discoid, producing 1 to several stems. Stems slightly compressed, verrucose with branch scars, to 12 cm long and 2-4 mm broad, bearing 1 to several main branches near the apex. Branches completely distichous; axes strongly winged, 5-12 mm broad with a prominent midrib, producing alternately from the edges simple, or more frequently divided, laterals, which are not, or only slightly, contracted at the base and taper evenly to narrow acute apices. Vesicles borne in the axils of the laterals or on the upper ramuli, petiolate, spherical, mutic, or rarely with a slender mucro up to 1 cm long, up to 6 mm in diameter. Receptacles racemose on the upper ramuli, simple or sometimes furcate, petiolate, linear lanceolate, smooth and terete, up to 6 mm long and ½-1 mm broad.

Type locality.—"North shores of New Holland".

Type.—British Museum (N.H.).

Distribution.—From Rottnest I., W.A., around northern Australia to Keppel Bay (Rockhampton), Qld.; with an isolated occurrence at Wallaroo, in Spencer's Gulf, S.A. Known also from New Caledonia.

The type, figured by Turner, is a young and fragmentary plant, and *S. decurrens* in the past has applied mainly to juvenile plants. J. Agardh's *S. scabripes* represents the older, more divided, and fertile plant. Occasionally old plants of *S. peronii* have basal laterals branched similarly to *S. decurrens* but not the tapering acute apices, and young plants of *S. peronii* have simple, distinctive laterals.

Sargassum peronii (Mertens) C. Agardh, Sp. Algarum **1:** 43 (1821); Syst. Algarum 308 (1824); J. Agardh, Sp. Gen. Ordines Algarum **1:** 284 (1848); Acta Univ. Lund. **9:** 54 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 47, pl. 15, fig. 1 (1889); De Toni, Sylloge Algarum **3:** 12 (1895); Grunow, Verh. zool.-bot. Ges. Wien **65:** 333 (1915); Sonder, Alg. trop. Aust. 7 (1871); Reinbold, Monogr. Siboga Exped. 59*a*: 153 (1913)

Fig. 1*a, b;* Plate 1, Figs. 1 and 2

Fucus peronii Mertens, Mém. Mus. Hist. Nat. Paris **5:** 175, pl. 13 (1819); Turner, Fuci Plant. Gen. Bot. **4:** pl. 247 (1819).

Sargassum boryi C. Agardh, Syst. Algarum 308 (1824); J. Agardh, Sp. Gen. Ordines Algarum **1:** 285 (1848); Acta Univ. Lund. **9:** 55 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 47, pl. 3 (1889); De Toni, Sylloge Algarum **3:** 13 (1895); Grunow, Verh. zool.-bot. Ges. Wien **65:** 334 (1915).

Pterocaulon peronii Kützing, Phycol. General. 360 (1843); Sp. Algarum 606 (1849); Tab. Phycol. pl. 65 (1860).

Pterocaulon boryi Kützing, Phycol. General. 360 (1843); Sp. Algarum 606 (1849).

Stems slightly compressed, to 10 cm long and 1-3 mm broad, verrucose with old branch scars, bearing from the upper edges several distichous, pinnate main branches, to 40 cm long. Branch axes broadly winged, 5-12 mm wide below with a prominent midrib, tapering evenly above and bearing, when young, alternate simple laterals which are contracted at the base, 2-5 cm long and 2-8 mm broad. Laterals on older plants, both larger ones at the base and young ones above, occasionally branched, but invariably with some simple laterals present. Secondary branches arising in axils of main branch laterals (which are lost on older plants), alternate, pinnate, distichous, with simple or rarely divided laterals up to 2 cm long and 3-4 mm broad. Cryptostomata in a line on each side of smaller laterals, irregularly scattered on larger laterals, often dense. Vesicles numerous, borne regularly in axils of each lateral on the main and secondary branches, spherical, shortly petiolate, mutic, up to 4 mm diameter. Receptacles distichous, simple or furcate, terete and smooth, linear lanceolate, 3-8 mm long and ½-1 mm broad.

Type locality.—"Nov. Holl. Littus occident."

Type.—Paris Museum.

Distribution.—From Rockingham (just south of Fremantle), W.A., around northern Australia to Rockhampton, Qld.; Aru Is. and New Caledonia.

Turner's and Mertens's descriptions were both published in 1819, Turner's from a specimen (now in Kew Herbarium) sent him by Mertens.

The type of *S. peronii* is a young plant, with the main branch laterals still present, and without receptacles. In older plants these laterals are often lost, and secondary branches develop from the axils of the laterals, later forming receptacles. This is the plant described by C. Agardh as *S. boryi*. An excellent set of specimens collected by R. L. Specht in Arnhem Land (now in Adelaide University Herbarium) shows these growth stages clearly.

S. peronii differs from *S. decurrens* in possessing more definite laterals, which are contracted at the base and usually simple, though sometimes divided. Some simple laterals will always be found. The laterals of *S. decurrens* are always several times divided and taper from the base into narrow acute segments; simple laterals are rarely, if ever, found.

Grunow (1915, p. 334) described two varieties, var. *lanceolata* and var. *intermedia*, of *S. peronii*, and under *S. boryi* he described (1915, pp. 334, 335) var. *angustissima* and forma *neocaledonica*. These appear to be only developmental stages or ecological variations and not worth recognizing.

Sargassum heteromorphum J. Agardh, Acta Univ. Lund. **9**: 60 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 42, pl. 1 (1889); De Toni, Sylloge Algarum 3: 8 (1895); Grunow, Verh. zool.-bot. Ges. Wien **65**: 332 (1915); Lucas, Seaweeds S. Aust. pt. **1**: 63, fig. 40 (1936)

Fig. 1*c;* Plate 2, Fig. 2

S. halitrichum J. Agardh, K. Svenska VetenskAkad. Handl. 23 (3): 43, pl. 13 (1889); De Toni, Sylloge Algarum 3: 9 (1895); Grunow, Verh. zool.-bot. Ges. Wien 65: 332 (1915); Lucas, Seaweeds S. Aust. pt. 1: 63 (1936).

Stem short (about 1 cm long), terete, arising from a lacerate discoid holdfast, and giving rise to 1 to several subdistichous main branches which are pinnate to bipinnate below with the lobes rounded to subacute, depending largely on age; segments up to 1 cm wide, with numerous cryptostomata. Lower parts changing fairly suddenly (usually) or more gradually to the upper slender, terete or slightly flattened, pinnate ramuli, about ½ mm broad. Upper ramuli bearing numerous petiolate vesicles, 1-2 (-3) mm diameter, with a prominent but acute and short apical mucro. Receptacles racemose, sessile or sometimes petiolate, terete, lanceolate, and often with a young receptacle near the base, 3-6 mm long when mature.

Type locality.—Georgetown, Tas. (Gunn).

Type.—Herbarium Agardh, Lund, No. 2626.

Distribution.—From Rottnest I., W.A., around southern Australia to Peterborough, Vic., and on the north coast (at least) of Tasmania. This species is found mainly on coasts of moderate wave action, or in bays; when growing on very exposed reefs or in deeper rock pools stunted or juvenile plants only may be found.

J. Agardh distinguished *S. heteromorphum* and his later-described *S. halitrichum* almost entirely on the basal parts, which he considered to be simply pinnate, with oblong and obtuse lobes in the former, and bipinnatifid with sublanceolate and acuminate lobes in the latter. He recognized only minor differences in the receptacles and vesicles.

In Herbarium Agardh, Lund, under *S. heteromorphum* are three sheets of Gunn's specimens from Tasmania, together with one other sheet. No plants have basal and upper parts actually attached, and J. Agardh's figure of basal parts is taken from one of two specimens on sheet 2627. The most suitable specimen to select as type, however, is No. 2626, where upper and lower parts are on one sheet.

Under *S. halitrichum* in Herbarium Agardh is only one specimen with basal and upper parts (No. 2635), which J. Agardh figured, and this is taken as the type. Areschoug's specimens comprise only upper parts and might belong to other species. The specimen shown in Plate 2, Figure 2, is identical with, but better developed than, the type of *S. halitrichum.*

There appear to be no real differences between *S. heteromorphum* and *S. halitrichum.* The form of the basal parts depends largely on the age of the plant and probably also on the habitat. Young basal parts are less divided and have rounded lobes; as the plant develops these become more branched and often bipinnate, with subacute apices. Considerable variation may be found on one specimen. The upper parts are similar in both cases, and also very similar to those in *S. sonderi* and *S. decipiens.*

S. australe Kützing (1861, Plate 43) was described from Herbarium Sonder (now in Melbourne National Herbarium), but this specimen could not be located. J. Agardh and Grunow doubtfully placed it under *S. halitrichum,* but as the figure shows only upper parts the name is best rejected as a nomen dubium.

Sargassum sonderi (J. Agardh) J. Agardh, Acta Univ. Lund. **9**: 59 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 44, pl. 14, figs. 1-2 (1889); De Toni, Sylloge Algarum **3**: 10 (1895)

Fig. 1*d;* Plate 3, Figs. 1 and 2

Cystophora sonderi J. Agardh, Sp. Gen. Ordines Algarum 1: 247 (1848); Harvey, Phycol. Aust. 5: pl. 243 (?) (no basal parts) (1860).

S. linearifolium sens. J. Agardh, Acta Univ. Lund. **9**: 57 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 45, pl. 14, fig. 3 (1889); Grunow, Verh. zool.-bot. Ges. Wien **65**: 333 (1915); Lucas, Seaweeds S. Aust. pt. 1: 63 (1936).

Not *S. flaccidum* Sonder in Lehmann, Pl. Preissianae 2: 164 (1846); Linnaea **25**: 668 (1852); Linnaea **26**: 511 (1853); which are largely *S. decipiens* (see below), except for the type of *S. sonderi.* Grunow's (1915, p. 332) description probably applies to *S. decipiens.*

Holdfast discoid, producing 1 to several stout, compressed stems to 10 cm (or more) high and 2-5 mm across, bare below except for prominent branch scars. Upper part of stem bearing several much divided main branches; axes of main branches angular but not flattened, bearing below pinnate linear laterals to 5-6 cm long, with segments 1-3 cm long and 2-4 (-5) mm broad. When mature, main branches developing further, bearing above crowded, much divided, filiform ramuli, with spherical, petiolate vesicles 1-2 (-3) mm diameter, with or without a slender apical mucro. Receptacles on upper ramuli, racemose, shortly lanceolate, terete, and smooth, 1-2 mm long and about ½ mm broad (possibly larger when fully mature).

Type locality.—Western Australia (Preiss), probably near Fremantle.

Type.—Herbarium Agardh, Lund, No. 2043.

Distribution.—From south-west Western Australia (Fremantle?) along southern Australia to Wilson's Promontory, Vic., and in Tasmania. On Kangaroo I. plants with mature upper parts are only found in the drift, while those in rock pools on reefs consist only of the immature basal parts. It appears to be mainly a sublittoral species of rough to moderately exposed coasts.

J. Agardh's original description (1848, p. 247) mentions specimens of Preiss from Western Australia and of Areschoug from Port Phillip. The latter specimen is not in Herbarium Agardh, and the Preiss specimen (No. 2043) is selected as the type. It consists of three pieces, two of upper parts and one lower part of a plant, which agree well with J. Agardh's concept and that expressed above. However, under *S. sonderi* J. Agardh placed some specimens of *S. decipiens.*

S. sonderi is based on one of Sonder's specimens from Preiss which he had named *S. flaccidum.* All the Preiss material in Lund (excluding No. 2043) and in Melbourne National Herbarium, however, is *S. decipiens,* so that J. Agardh apparently had the only distinct specimen in this collection for his type of *S. sonderi.*

J. Agardh's concept and specimens of *S. linearifolium* are also *S. sonderi,* though mainly only the juvenile or basal state. This is further discussed under *S. linearifolium.*

The upper mature parts of *S. sonderi* are very similar to those of *S. decipiens,* and these species are virtually indistinguishable without the lower parts. The receptacles of *S. sonderi* may be smaller, and there appear to be many fewer cryptostomata (often none) than in *S. decipiens,* but these are variable factors.

Harvey's specimens (No. 15 Algae Aus. Exsicc.) and his figure (1863, Plate 243) show only the upper fertile parts, and cannot be identified with certainty. They might equally well be *S. decipiens.*

Grunow's description (1915, p. 332) seems to apply to *S. decipiens;* what his var.? *immixta* from Rockingham, Qld., is must remain doubtful, but it is probably not a form of *S. sonderi* or *S. decipiens.*

Sargassum decipiens (R. Brown in Turner) J. Agardh, Acta Univ. Lund. **9**: 63 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 51 (1889); De Toni, Sylloge Algarum **3**: 15 (1895); Grunow, Verh. zool.-bot. Ges. Wien **66**: 335 (1915). All these references apply in part only.

Fig. 1*e, f;* Plate 4, Fig. 1

Fucus decipiens R. Brown in Turner, Fuci Plant. Gen. Bot. **3**: pl. 166*a, c, d* (not *b*) (1811).

S. muriculatum J. Agardh, Acta Univ. Lund. **9**: 58 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 44, pl. 14, fig. 2 (1889); De Toni, Sylloge Algarum **3**: 10 (1895); Grunow, Verh. zool.-bot. Ges. Wien **66**: 333 (1915); Womersley, Trans. Roy. Soc. S. Aust. **72**: 155 (1948).

S. sonderi Grunow, Verh. zool.-bot. Ges. Wien **66**: 332 (probably) (1915).

The following references apply in part (see discussion below):

Cystoseira decipiens (R. Br.) C. Agardh, Sp. Algarum **1**: 76 (1821); Syst. Algarum 290 (1824).

Cystophora decipiens (R. Br.) J. Agardh, Sp. Gen. Ordines Algarum 249 (1848).

Blossevillea decipiens (R. Br.) Kützing, Sp. Algarum 630 (1849).

Sargassum flaccidum Sonder, Pl. Preissianae **2**: 164 (1846).

Cystophyllum flaccidum Sonder, Linnaea **25**: 668 (1852); **26**: 511 (1853).

Holdfast discoid, producing 1 to a few stout, strongly compressed stems, to several centimetres in length and 3-6 mm broad, with prominent branch scars. Upper part of stem with several main branches to 40 cm long, bearing simple or branched laterals on all sides below, and much divided above; lower laterals flattened to almost terete, 1-4 cm long and ½-2 mm broad, simple or once or twice divided, densely clustered and often with prominent cryptostomata; upper parts much divided into filiform, terete ramuli 1-3 cm long with numerous cryptostomata. Vesicles developing in adult plants in late winter, 1-2 (-3) mm in diameter, spherical to slightly ovoid, petiolate, and with a small mucro. Receptacles racemose, petiolate, ovate to lanceolate, smooth to somewhat verrucose.

Type locality.—Port Dalrymple (Tamar estuary), Tas.

Type.—British Museum (N.H.).

Distribution.—From Western Australia (Cottesloe?) around southern Australia to Peterborough, Vic., and in Tasmania. Common on reefs at an upper sublittoral level or in rock pools in South Australia, on rough and moderately exposed coasts.

The seasonal development of *S. decipiens* has been discussed previously (Womersley 1948, p. 155, as *S. muriculatum*). During summer, the plants are short (to 10-12 cm high) and appear stunted, the branch axes being very densely covered with terete or slightly compressed laterals. Further growth commences in March or early April, and during winter the fertile fronds develop, bearing vesicles and receptacles in late winter and reaching a height of 40 cm. In November or early December the fertile fronds disintegrate, leaving only the old branch axes, which may persist for a few months.

The type of *Fucus decipiens* is in the British Museum (N.H.). Brown placed two specimens, actually different species, on the one sheet. The one on the left Turner described and figured as adult *F. decipiens*, and as he clearly based his concept of the species on this specimen, it must be taken as the type. The right-hand specimen ("*b*" in Turner's plate) he regarded as a juvenile plant, with much broader basal leaves than the adult. J. Agardh, however, retained the name *decipiens* for the "juvenile" plant, referring the adult specimen to *S. turneri* (a variety of *S. trichophyllum*). Much confusion has arisen from this error, as J. Agardh has been followed by most subsequent authors. All J. Agardh's specimens under *S. decipiens* in Lund, and his descriptions of this species, are, or apply to, *S. varians* Sonder, while he redescribed the summer state of *S. decipiens* as *S. muriculatum.*

Sargassum howeanum Lucas, Proc. Linn. Soc. N.S.W. **60**: 207, pl. 6, fig. 2 (1935)

Holdfast discoid. Stem short (about 1 cm long), terete and nodulose, producing 1 to several main branches up to 40 cm long. No distinct basal laterals developed. Main branches with angular axes, much divided into crowded, filiform, pinnate ramuli on all sides, bearing spherical, petiolate, mutic vesicles 1-3 (-4) mm in diameter. Receptacles "fusiform, 2-3 mm long, stipitate, smooth, simple or branched" (after Lucas).

Type locality.—Lord Howe I.

Type.—Lucas Herbarium, C.S.I.R.O., Canberra. Isotype in Adelaide University Herbarium.

Distribution.—Lord Howe I., where it is common on the lagoon floor (Lucas).

Lucas compared this species to *S. sonderi;* it is, however, closer to *S. decipiens*, differing from the latter in having a terete stem, in the apparent absence of any distinct lower laterals, and in the mutic vesicles.

Sargassum varians Sonder, Bot. Z. 3: 51 (1845); Pl. Preissianae 2: 163 (1846); Linnaea 25: 671 (1852); **26**: 512 (1853); J. Agardh, Sp. Gen. Ordines Algarum **1**: 287 (1848); Acta Univ. Lund. **9**: 64 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 49, pl. 16, figs. 1-8 (1889); De Toni, Sylloge Algarum 3: 14 (1895); Grunow, Verh. zool.-bot. Ges. Wien **65**: 335 (1915); Kützing, Sp. Algarum 617 (1849); Tab. Phycol. **11**: pl. 36 (1861); Lucas, Seaweeds S. Aust. pt. **1**: 64 (1936)

Fig. 1*g, h;* Plate 4, Fig. 2

S. decipiens sens. J. Agardh, Acta Univ. Lund. **9**: 63 (1872); K. Svenska VetenskAkad. Handl. **23** (3): 51, pl. 15, fig. 3 (1889); Grunow, Verh. zool.-bot. Ges. Wien **65**: 335 (1915).

Holdfast discoid, with (usually) a single compressed stem to 6 cm high and 2-4 mm broad, with prominent lateral, alternate branch scars. Upper part of stem with 1 to several main branches up to 40 cm in length. Axes of main branches strongly compressed below, producing simple linear laterals which soon develop into reflexed pinnate laterals, arising from near the edge of the branch axis; pinnate laterals 3-8 cm long, segments 2-4 mm broad, with rounded or acute apices and usually with cryptostomata. Lower laterals changing suddenly or gradually to the upper, filiform, pinnate ramuli, bearing petiolate, spherical vesicles 2-6 mm in diameter, mutic or with a small and slender to longer and compressed mucro (to 2 cm long and 2 mm broad). Receptacles crowded, each in the axil of a simple or furcate ramulus, ovate to lanceolate, smooth, terete, from sessile to shortly petiolate, 1-3 mm long and ½-1 mm broad. Dioecious, the female receptacles being somewhat shorter and in denser clusters than the male.

Type locality.—Western Australia (Preiss) — probably near Fremantle.

Type.—Melbourne National Herbarium (see Plate 4, Fig. 2).

Distribution.—From Cottesloe, W.A., to Wilson's Promontory, Vic., and in Tasmania (north coast and probably elsewhere). Often common in the drift from deep water on rough to moderately exposed coasts, occasionally found in rock pools.

The distinctive features of *S. varians* are the large vesicles (found also in *S. verruculosum*), the flat lower branch axes producing retrofract pinnate laterals, and the compressed stem. The latter feature in particular distinguishes it from *S. verruculosum.*

J. Agardh's concept of *S. decipiens* applies to *S. varians* Sonder, as discussed under the former species.

In a few specimens from Yallingup and Point D'Entrecasteaux, W.A., the main branches of young plants were unusually well developed, reaching 20 cm in length yet with simple linear laterals to 5 cm long and 2-3 mm wide. This gave the main branches a simply pinnate appearance; later, however, branching occurred, and vesicles arose in the axils of the laterals.

Sargassum verruculosum (Mertens) C. Agardh, Sp. Algarum **1:** 26 (1821); Syst. Algarum 302 (1824); J. Agardh, Acta Univ. Lund. **9:** 61 (1872); K. Svenska VetenskAkad. Handl. 23 (3): 53, pl. 18, figs. 1-6 (1889); De Toni, Sylloge Algarum 3: 16 (1895); Grunow, Verh. zool.-bot. Ges. Wien **65:** 336 (1915); Kützing, Sp. Algarum 617 (1849); Tab. Phycol. **11:** pl. 34, fig. 2 (1861); Lucas, Seaweeds S. Aust. pt. **1:** 64 (1936); May, Proc. Linn. Soc. N.S.W. **64:** 202 (1939)

Figs. 1*i*, *j*; Plate 5, Figs. 1 and 2

Fucus verruculosus Mertens, Mém. Mus. Hist. Nat. Paris 5: 186, pl. 15 (1819).

Cystophora verruculosa (Mert.) J. Agardh, Sp. Gen. Ordines Algarum 1: 248 (1848); Sonder, Linnaea 26: 511 (1853).

Sargassum raoulii Hooker and Harvey, Lond. J. Bot. 4: 523 (1845); Harvey in Hooker, Bot. Antarct. Voyage 2 (2): 212 (1855); Phycol. Aust. 2: pl. 110 (1859); in Hooker, Bot. Antarct. Voyage 3 (2): 282 (1860); Kützing, Sp. Algarum 616 (1849).

Sargassum capillaceum Hooker and Harvey, Lond. J. Bot. 6: 414 (1847); Kützing, Sp. Algarum 617 (1849).

Sargassum adenophyllum Harvey in Hooker, Bot. Antarct. Voyage 2 (2): 212 (1855).

Sargassum trichophyllum J. Agardh, K. Svenska VetenskAkad. Handl. 23 (3): 52, pl. 17, figs. 10-12 (1889); De Toni, Sylloge Algarum 3: 16 (1895); Grunow, Verh. zool.-bot. Ges. Wien 65: 336 (1915); Lucas, Seaweeds S. Aust. pt. 1: 64 (1936).

Holdfast discoid. Stem terete, but with prominent branch scars, producing from near the apex 1 to several long, usually slender and much divided main branches, primarily distichous but sometimes tending to appear almost radial. Branch axes compressed below, with irregularly pinnate laterals up to 4-5 cm long, and segments 1-3 mm broad; cryptostomata usually present; bases of laterals usually retrofract. Lower laterals frequently lost in old plants, leaving a bare flexuous axis to the main branches. Upper ramuli filiform, dense, from rigidly dichotomous to laxly pinnate-dichotomous in older plants, with or without prominent cryptostomata, bearing numerous large, prominent vesicles of varying sizes up to 1 cm diameter, mutic or with a slender, usually short mucro (but up to 1 cm long, bearing cryptostomata when long). Receptacles borne on upper ramuli, 3-5 mm long and about 1 mm broad, lanceolate and slightly torulose, subsessile to petiolate, occasionally branched or with short sterile projections from the receptacle.

Type locality.—Western Australia.

Type.—Paris Museum.

Distribution.—From Western Australia (probably the south-west) around southern Australia to Maroubra Bay, N.S.W., and around Tasmania; New Zealand. Mainly on rough coasts but extending to relatively calm habitats, where the largest plants occur. Mature plants are usually found in drift from the sublittoral, while forms on reefs or in deeper pools comprise the juvenile or basal parts only.

S. verruculosum is a very variable species, distinguished by the terete (though with prominent branch scars) stem, the very large abundant vesicles, and the flattened lower axes of the main branches, together with the lower retrofract laterals and flexuose appearance of the old branch axes.

The general form of the plant, its size, abundance and prominence of cryptostomata, and abundance of vesicles are all variable factors, mainly due to habitat and age. Plants from reef pools are generally small and relatively stout, with prominent cryptostomata, often without vesicles, and may consist only of the branches and lower laterals (Plate 5, Fig. 1). Deeper-water plants (and ones during winter) are larger, more branched with finer ramuli, with few cryptostomata and large and abundant vesicles. These latter plants correspond to Hooker and Harvey's *S. capillaceum.*

S. trichophyllum has usually been separated from *S. verruculosum,* but the distinction cannot be maintained. J. Agardh recognized two varieties of *S. trichophyllum* — var. *turneri,* which was based on Turner's

S. decipiens, though his figures may be of *S. verruculosum;* and var. *corymbosum*, the type of which (Herb. Agardh No. 2767) is certainly only a form of *S. verruculosum.*

SPECIES EXCLUDED FROM PHYLLOTRICHIA

Sargassum linearifolium (Turner) C. Agardh, Sp. Algarum **1:** 24 (1821); Syst. Algarum 303 (1824); Kützing, Sp. Algarum 612 (1849); Tab. Phycol. **11:** pl. 18 (1861)

Fucus linearifolius Turner, Fuci Plant. Gen. Bot. 2: 106 pl. 111 (1809).

This species has generally been included in *Phyllotrichia.* Turner gave the locality of the type specimen (in Kew Herbarium) as "western coast of New Holland", but on the type sheet is "South Sea. Menzies 1788". The type sheet consists of three specimens, the centre one being figured by Turner. They represent only the upper branches of plants, without basal parts. The main branches bear 2 rows of tufted leaves and receptacles; the leaves are linear, up to 4 cm long, and only ½-1 mm wide, with a prominent midrib and scattered, sparse cryptostomata. The receptacles are densely clustered in the leaf axils, simple or furcate (usually once furcate, sometimes twice), terete, and smooth except for the swollen conceptacles. Vesicles are absent.

Plants which are almost certainly identical with the type material occur on parts of the South Australian coast. These show distinct basal leaves, broader (to 4-5 mm) and longer than the upper ones, and often branched. During summer (December to March) only the basal parts are present, with leaves normally branched two to four times. Preliminary observations indicate that the basal leaves are lost before the upper fertile fronds (which have only simple leaves) develop during winter. The receptacles in fully developed plants are densely clustered and up to four or five times dichotomous, while vesicles may develop on old fronds. The two rows of "leaf tufts" in the type are more marked than in most specimens.

Although the branched basal leaves in the young or summer state of *S. linearifolium* point to affinity with *Phyllotrichia*, the always simple and flattened upper leaves, the branched receptacles, and the general aspect of the plant are distinctly those of *Arthrophycus.* While further study is needed, it seems best to class *S. linearifolium* as a species of *Arthrophycus* which is unusual in having branched basal leaves during summer.

Almost every specimen J. Agardh referred to *S. linearifolium* (in Herbarium Agardh) belongs to *S. sonderi*, being mostly the basal parts of this species. The only true *S. linearifolium* in Herbarium Agardh is a fragment of Menzies' original collection. J. Agardh's figures (1889, Plate 14, Figs. 3-7) also clearly refer to *S. sonderi.* C. Agardh's descriptions (1821, p. 24; 1824, p. 303) probably apply to the type; J. Agardh's (1848, p. 296) where he placed it in *Arthrophycus* does in part, but his

1872 (p. 57) and 1889 (p. 45) descriptions are incorrect. Kützing's description and figures are probably based on Turner's and are reliable, but May's (1939, p. 202) description is incorrect.

S. linearifolium probably occurs generally along southern Australia, from the south-west to New South Wales. It is common in reef pools on parts of the South Australian coast.

ACKNOWLEDGMENTS

Acknowledgment is made to the directors of the Herbarium, Royal Botanic Gardens, Kew; the British Museum (Natural History), London; the Botanical Museum, Lund; and the Laboratoire de Cryptogamie, Muséum d'Histoire Naturelle, Paris, for facilities and permission to examine algal types, and also to the directors of the various Australian herbaria (listed in the Introduction) for the loan of specimens of *Sargassum*.

REFERENCES

AGARDH, C. A. (1821).—"Species Algarum." Vol. 1. (Lund.)

AGARDH, C. A. (1824).—"Systema Algarum." (Lund.)

AGARDH, J. G. (1848).—"Species Genera et Ordines Algarum." Vol. 1. (Lund.)

AGARDH, J. G. (1872).—Till algernes systematik. Nya bidrag. III. *Acta Univ. Lund.* **9**: 51-71.

AGARDH, J. G. (1889).—Species Sargassorum australiae. *K. Svenska VetenskAkad. Handl.* **23** (3): 1-133, pl. 1-31.

DE TONI, G. B. (1895).—"Sylloge Algarum." Vol. 3, Fucoidaea.

GRUNOW, A. (1915).—Additamenta ad cognitionem Sargassorum. *Verh. zool.-bot. Ges. Wien* **65**: 329-448.

GRUNOW, A. (1916).—Additamenta ad cognitionem Sargassorum. *Verh. zool.-bot. Ges. Wien* **66**: 1-48, 136-85.

HARVEY, W. H. (1855).—"Algae" *in* J. D. Hooker: "The Botany of the Antarctic Voyage. Vol. 2. Flora Novae Zelandiae." Part 2: 211-66.

HARVEY, W. H. (1859).—"Phycologia Australica". **2**: pl. 61-120.

HARVEY, W. H. (1860*a*).—"Phycologia Australica." **3**: pl. 121-80.

HARVEY, W. H. (1860*b*).—"Algae" *in* J. D. Hooker: "The Botany of the Antarctic Voyage." Vol. III. Flora Tasmaniae, Pt. 2, 282-343.

HARVEY, W. H. (1863).—"Phycologia Australica." **5**: pl. 241-300.

HOOKER, J. D., and HARVEY, W. H. (1845).—Algae Novae Zelandiae. *Lond. J. Bot.* **4**: 521-51.

HOOKER, J. D., and HARVEY, W. H. (1847).—Algae Tasmanicae. *Lond. J. Bot.* **6**: 397-417.

KUTZING, F. T. (1843).—"Phycologia Generalis." (Leipzig.)

KUTZING, F. T. (1849).—"Species Algarum." (Leipzig.)

KUTZING, F. T. (1860).—"Tabulae Phycologicae." Vol. 10.

KUTZING, F. T. (1861).—"Tabulae Phycologicae." Vol. 11.

LUCAS, A. H. S. (1935).—The marine algae of Lord Howe Island. *Proc. Linn. Soc. N.S.W.* **60**: 194-232.

LUCAS, A. H. S. (1936).—"The Seaweeds of South Australia." Part 1. (Adelaide.)

MAY, VALERIE (1939).—A key to the marine algae of New South Wales. Part 2. Melanophyceae (Phaeophyceae). *Proc. Linn. Soc. N.S.W.* **64**: 191-215.

MAY, VALERIE (1953).—Some marine algae from New Caledonia collected by Mrs. R. Catala. *Contrib. N.S.W. Nat. Herb.* **2**: 38-66.

MERTENS, J. C. (1819).—Mémoire sur plusiers espèces de *Fucus*, nouvelles ou peu connues, observées dans la collection du Muséum. *Mém. Mus. Hist. Nat. Paris.* **5**: 172-90, pl. 13-15.

REINBOLD, T. (1913).—"Sargassum" *in* W. v. Bosse: Liste des Algues du Siboga. I. Myxophyceae, Chlorophyceae, Phaeophyceae. *Monogr. Siboga Exped.* **59***a*: 150-74.

SETCHELL, W. A. (1931).—Hong Kong seaweeds. II. *Hongkong Nat.* **2**: 237-53.

SETCHELL, W. A. (1933).—Hong Kong seaweeds. III. Sargassaceae. *Hongkong Nat.* Suppl. No. 2: 33-49, pl. 3-20.

SETCHELL, W. A. (1935).—Hong Kong seaweeds. IV. Sargassaceae. *Hongkong Nat.* Suppl. No. 4: 1-24, pl. 1-17.

SETCHELL, W. A. (1936).—Hong Kong seaweeds. V. Sargassaceae. *Hongkong Nat.* Suppl. No. 5: 1-20, pl. 1-8.

SONDER, O. W. (1845).—Nova algarum genera et species quas in itinere ad oras occidentales Novae Hollandiae collegit L. Preiss. *Bot. Z.* **3**: 49-57.

SONDER, O. W. (1846).—"Algae" *in* Lehmann, "Plantae Preissianae". **2** : 148-95.

SONDER, O. W. (1852).—Plantae Muellerianae. Algae. *Linnaea* **25**: 657-709.

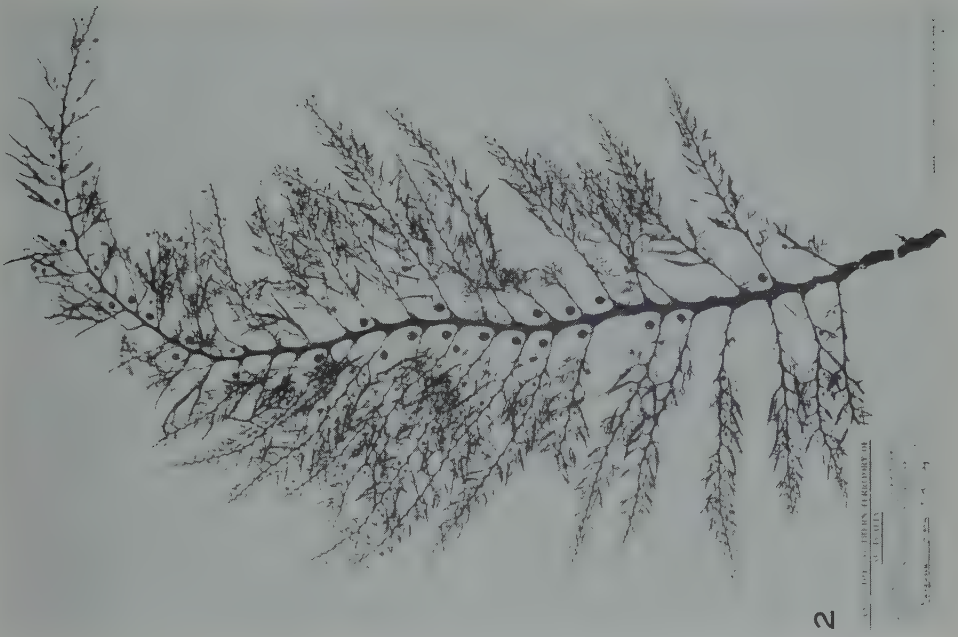
SONDER, O. W. (1853).—Algae annis 1852 et 1853 collectae. *Linnaea* **26**: 506-28.

SONDER, O. W. (1871).—"Die Algen des tropischen Australiens."

TURNER, D. (1808-1819).—"Fuci Sive Plantarum Fucorum Generi a Botanicis Ascriptarum Icones Descriptiones et Historia." (London.) 1808, **1**: pl. 1-71. 1809, **2**: pl. 72-134. 1811, **3**: pl. 135-96. 1819, **4**: pl. 197-258.

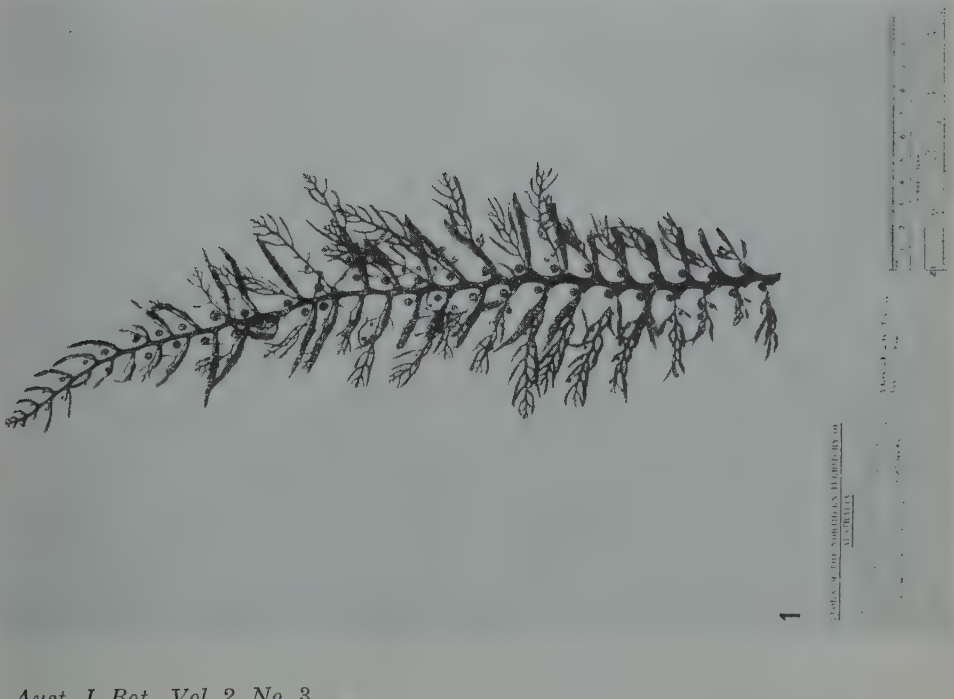
WOMERSLEY, H. B. S. (1948).—The marine algae of Kangaroo Island. II. The Pennington Bay region. *Trans. Roy. Soc. S. Aust.* **72**: 143-66, pl. 10-15.

AUSTRALIAN SPECIES OF PHYLLOTRICHIA



2

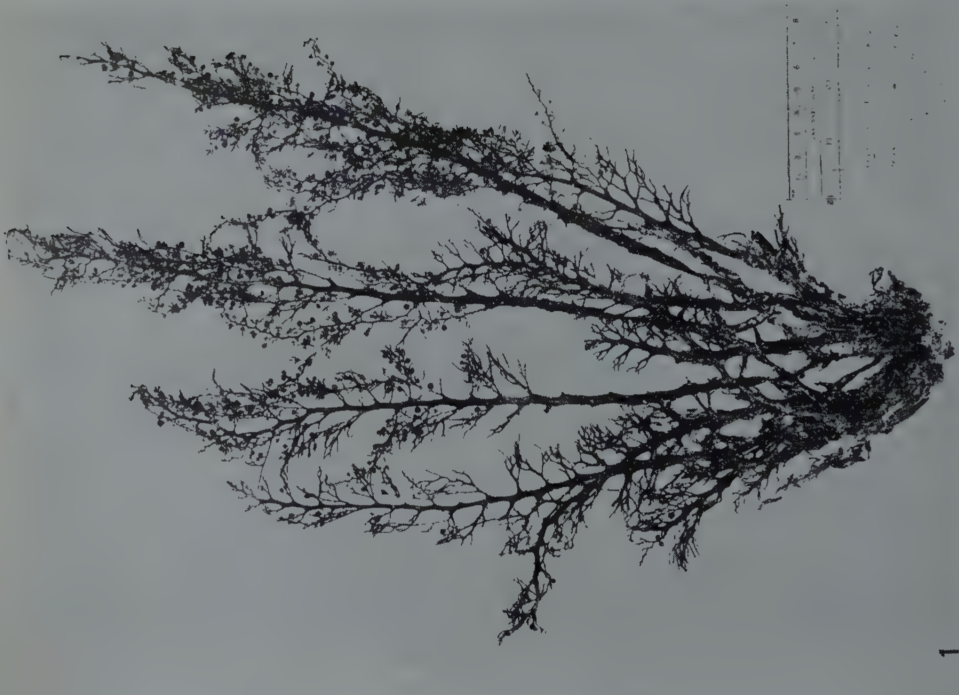
Fig. 2.—*S. peronii*: a mature fertile branch.



1

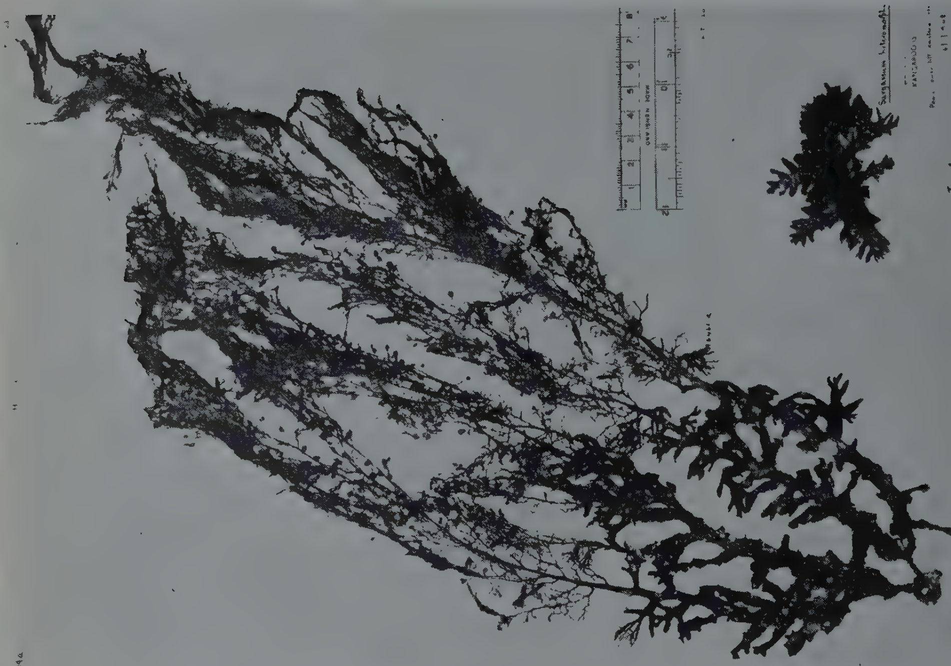
Fig. 1.—*S. peronii*: a young plant.

AUSTRALIAN SPECIES OF PHYLLOTRICHIA



1

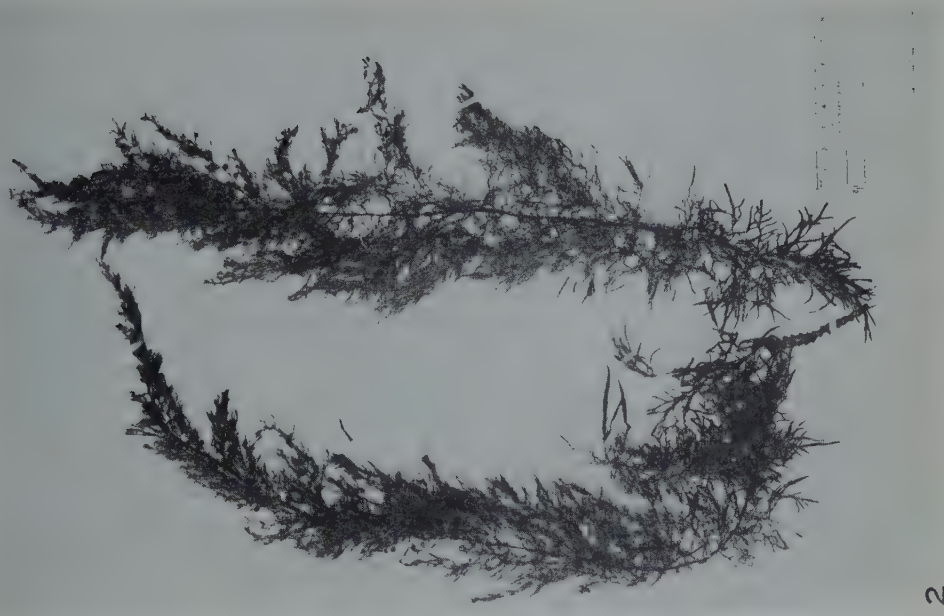
Fig. 1.—*S. decurrens*: a mature fertile plant.



2

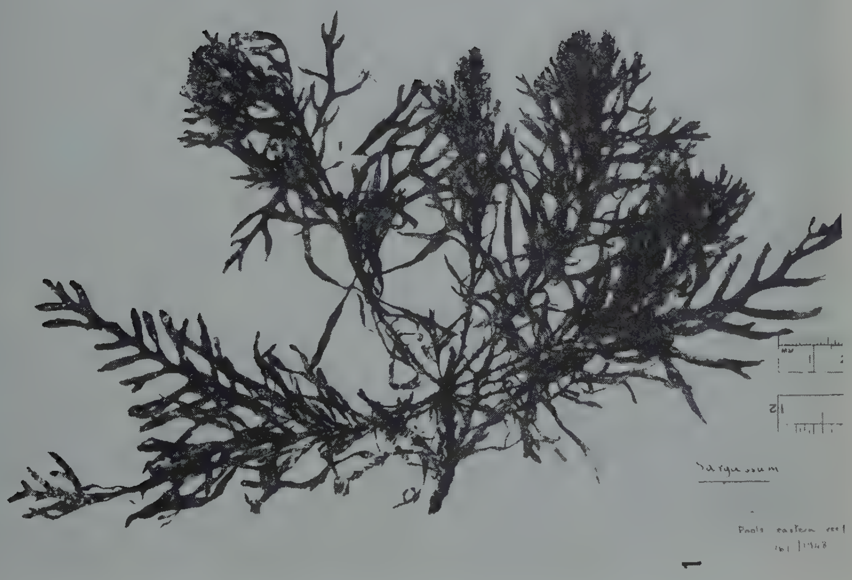
Fig. 2.—*S. heteromorphum*: a mature plant on the left, with a young rock pool form on the right.

AUSTRALIAN SPECIES OF PHYLLOTRICHIA



2

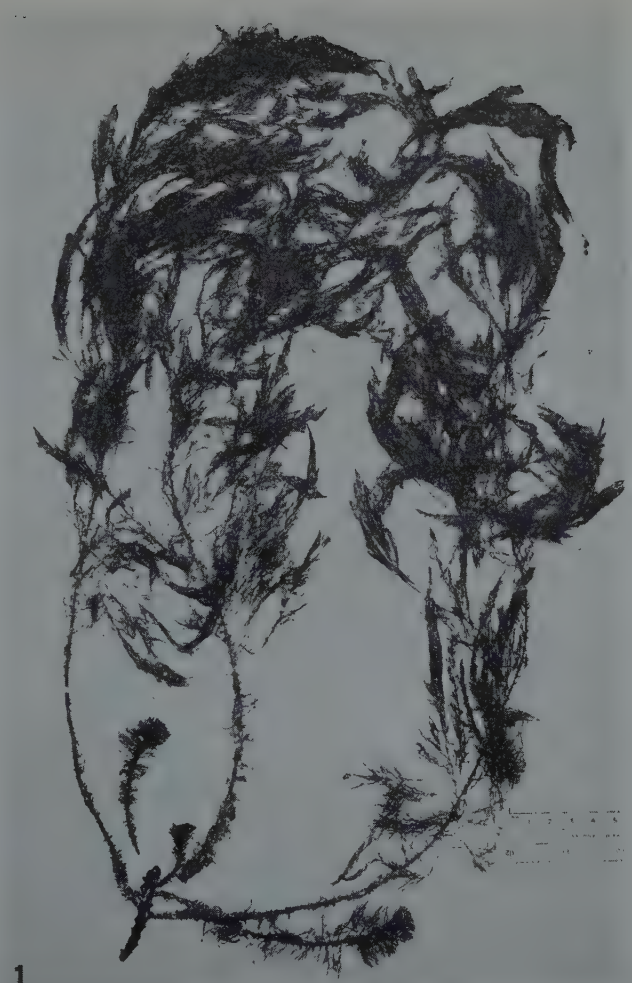
Fig. 2.—*S. sonderi*: a mature plant.


Sargassum
Pools eastern reef

1

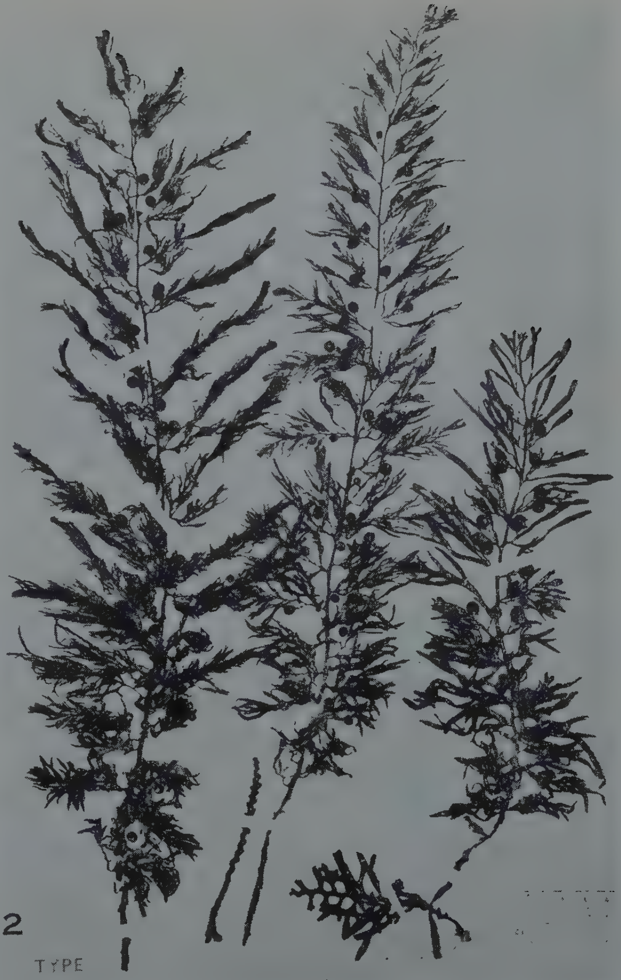
Fig. 1.—*S. sonderi*: a juvenile plant with well-developed main branches only.

AUSTRALIAN SPECIES OF PHYLLOTRICHIA



1

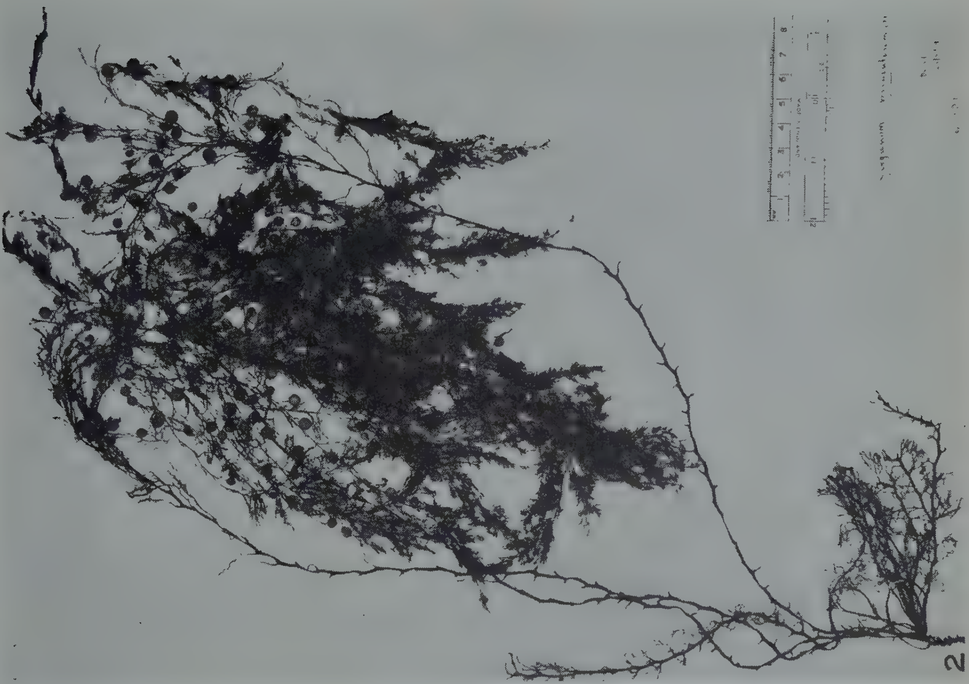
Fig. 1.—*S. decipiens*: a mature, fertile, vesiculate plant.



2

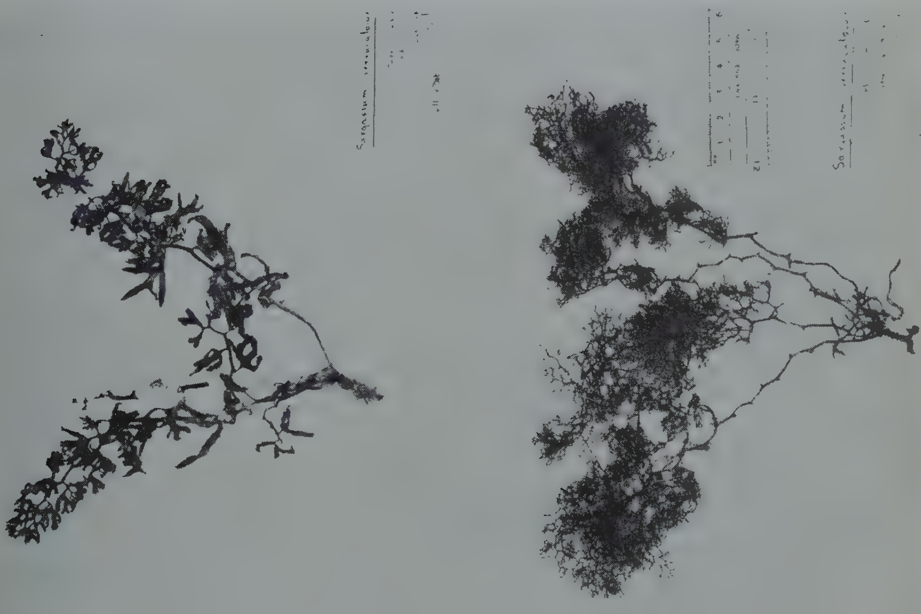
Fig. 2.—*S. varians*: the type sheet of Sonder.

AUSTRALIAN SPECIES OF PHYLLOTRICHIA



2

Fig. 2.—*S. verruculosum*: a mature, vesiculate plant.



1

Fig. 1.—*S. verruculosum*: two juvenile forms with lower parts only.

NEW SOIL FUNGI FROM AUSTRALIAN HEATHLAND: *ASPERGILLUS, PENICILLIUM, SPEGAZZINIA*

By ETHEL I. MCLENNAN*, SOPHIE C. DUCKER*, and L. B. THROWER†

(*Manuscript received April 23, 1954*)

Summary

Five new species of soil fungi are described and figured. These have been isolated from a sandy podzol supporting a characteristic heathland flora.

INTRODUCTION

During our studies on the ecology of fungi in the Australian heathland soils we have isolated repeatedly the forms discussed in this paper. Their morphology and growth characters are distinct from those of any described species. They have all been grown in the laboratory for a period of at least 2 years on a wide variety of media, and under diverse conditions. The descriptions of the fungi have been made from colonies grown on malt extract, Czapek's and Raulin's agar. The composition of the media employed is as follows:

(1) *Malt extract agar*.—Distilled water 1 l.; malt extract 20 g; dextrose 20 g; peptone 1.0 g; agar 25 g. The pH is approximately 4.7 and was not adjusted.

(2) *Czapek's solution agar*.—Distilled water 1 l.; sucrose 30 g; $NaNO_3$ 3.0 g; K_2HPO_4 1.0 g; $MgSO_4.7H_2O$ 0.5 g; KCl 0.5 g; $FeSO_4.7H_2O$ 0.01 g; agar 18 g. The pH was adjusted to 6.9 with NaOH.

(3) *Raulin's agar*.—Distilled water to 1.5 l.; sucrose 70 g; tartaric acid 4 g; ammonium tartrate 4 g; K_2CO_3 0.60 g; $MgCO_3$ 0.40 g; $(NH_4)_2SO_4$ 0.25 g; $ZnSO_4.7H_2O$ 0.07 g; $FeSO_4.7H_2O$ 0.07 g; K_2SiO_3 0.07 g; agar 27 g. The pH is approximately 3.9 and was adjusted to 6.9 with KOH.

Genus ASPERGILLUS Mich. ex Fr.

Aspergillus nutans sp. nov.

Coloniae in substratis differentibus multo variantes, in agaro Czapekii tarde crescentes, tenuissimae, translucidae, capitula conidiorum vix ulla efformantes; coloniae in agaro maltoso celeriter crescentes, floccosae, laxa textura, vinaceae, reverso bubalino margine pallidiore; conidiophoris e substrato et ex hyphis subsinuosis orientibus, 20-100 μ longis, membrana levi praeditis, septatis, cella infima in pedem densata, infra vesiculas abrupte nutantibus; vesiculis, 7-15 μ latis, globosis, hemisphaerico superiore sterigmatibus tecto, inferiore sterili; sterigmatibus in una serie nutantibus, 5-10 μ × 2-2.5 μ; conidiis globosis, 3-4 μ, glabris, coloratis.

---

* Botany Department, University of Melbourne.

† Botany Department, University of Melbourne; present address: Department of Agriculture, Stock, and Fisheries, Port Moresby, New Guinea.

Habitat: in solo arenoso acido, Australia.

Colonies on *malt* agar growing fairly rapidly, 7-8 cm in diameter in 14 days at 24°C. The colony has a loose-textured appearance with the upper surface floccose, vinaceous fawn (XL) to light russet vinaceous (XXXIX) in colour, fading towards the periphery. The reverse is warm buff to buck-thorn brown in age (XXV) with paler margin. Some isolations are more pronouncedly floccose on malt with a lighter sporing colour (pale ochraceous to light ochraceous buff (XXV)).

Colonies on *Czapek* solution agar show a very thin and transparent growth with no sporulating colour developing. The colonies measure 1-2 cm in diameter after 14 days at 24°C.

On *Raulin* agar the colony is slightly denser than on Czapek agar. Sporing heads are sparsely formed, giving a slight buff colour to the upper surface. The zoned reverse shows the sporing colour of the upper surface through the thin colony.

Morphology as on malt agar.—The conidiophores are borne either on trailing hyphae or direct from the substratum. They are variable in length, ranging from 20 to 100 μ; they are smooth-walled and septated and have a well-developed foot-cell. The vesicle is 7-15 μ broad and is sharply bent downwards, giving to the conidiophores a characteristic nodding appearance. The phialides are borne in a single series from the upper part of the vesicle, they lie parallel with one another, are variable in size from 5-10 μ long by 2.0-2.5 μ broad. They bear short, clumped, rather persistent conidial chains. The smooth and tinted conidia are globose, 3-4 μ in diameter. Perithecia have never been observed even in the newly isolated colonies.

Although slow in developing on the malt agar dilution plates used in our soil studies, it was isolated from all the soil horizons. It is the dominant species of the genus in the general soil, although in the rhizosphere and close to decaying plant tissue it is replaced by *A. fumigatus* Fres. The characters of the many isolates remained constant. The phialides are always in one series and the very characteristic swan-neck-like appearance of the conidiophores suggests that this fungus is an undescribed species of *Aspergillus*. The surface colour of the colonies on malt is similar to that noted for *A. carneus* (v. Tiegh.) Blockwitz, which belong to the *A. terreus* group, which is, however, characterized by crowded sterigmata borne in two series. *A. carneus* also grows well on Czapek agar with its growth more restricted on malt. The extremely sparse and thin growth on our isolates on Czapek is another feature which separates it from *A. carneus*. We therefore propose the trivial name *nutans* for this soil-inhabiting *Aspergillus*. A type culture (4B4) has been lodged in the Commonwealth Mycological Institute's collection, Kew, England.

Aspergillus viridi-nutans sp. nov.

Coloniae in agaro Czapekii, velutinae, salviavirides, margine lato albo viridimaculato; reverso viridicolorato; coloniae in agaro maltoso velutinae, cyaneo-virides, margine angusto albo; reverso pallido-brunneo, margine albo; conidiophoris e substrato et ex hyphis subsinuosis orientibus, membrana levi praeditis, saepe septatis; vesiculis in conidiophoris paucis erectis, sed saepius nutantibus; vesiculis, 7.5-15 μ; sterigmatibus in una serie, 6-7.5 μ; conidiis globosis, 2-2.5 μ, glabris, hyalino vel pallidoviridi colore.

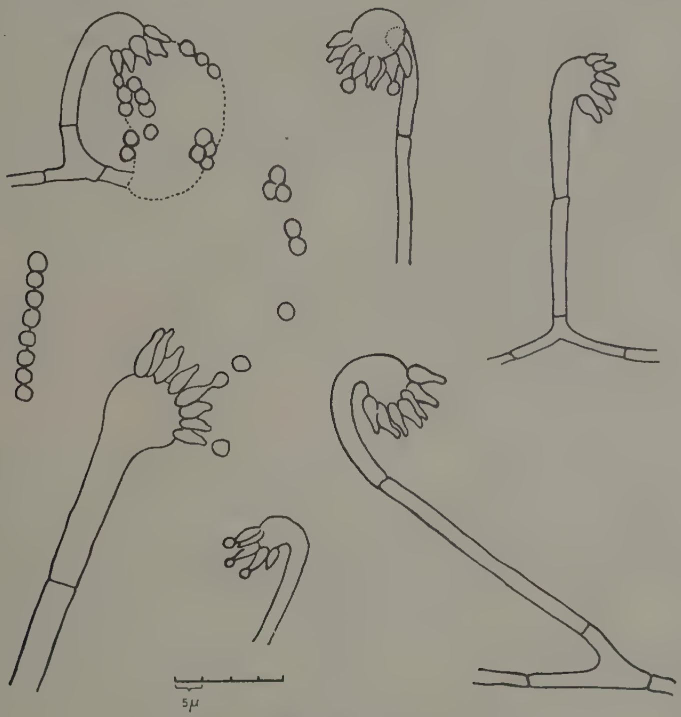


Fig. 1.—*Aspergillus nutans* McLennan & Ducker. Conidial heads and mature conidia. × 385. In this and other figures, all drawings have been made with the aid of a camera lucida at bench level.

Habitat: in faecibus *Oryctolagi cuniculi* L. et in solo arenoso acido, Australia.

Colonies on *malt* agar 4 cm in diameter after 14 days at 24°C. The surface was velvety, slightly zonate, and the colour close to Niagara green (XXXIII) with a narrow white margin. The reverse was coloured light brownish olive (XXX) with a white margin.

Colonies on *Czapek* agar after 14 days at 24°C were 3.5-4 cm in diameter and thinner than on malt agar. The centre of the colony was raised, the sporing colour was sage green (XLVII) to Pois green (XLI), beyond this was a region about 1 cm wide extending to the colony edge, which was white flecked with green. On the reverse the green shades showed through with a white margin.

On *Raulin's* agar the diameter after 14 days was 2 cm. The surface was extremely buckled and the colour approximately sage green (XLVII), with sporing occurring almost to the edge of the colony. The reverse was buckled and showed Vetiver green shades (XLVII).

Morphology as on malt agar.—The conidiophores may arise from the substrate or from trailing hyphae. The former measure 50 μ or more in length, but the latter vary from 20 to 35 μ. They were smooth-walled and often septate. Most of the vesicles measure 7.5-12 μ (av. 9 μ) in width, but in exceptional examples they range up to 15 μ wide. The arrangement of the vesicle and phialides is such as to present a "nodding" appearance. Although upright heads are often seen, the nodding type seems to predominate. Over the surface of the vesicle is borne a single series of phialides up to 12 in number, which measure 6-7.5 μ long. The globose conidia are smooth, hyaline to pale green, 2-2.5 μ in diameter.

A. viridi-nutans was isolated from the A horizon of the sandy podzol at Frankston and from rabbit dung at that location.

A type culture (Rab. 7) has been lodged in the collection of the C.M.I.

Aspergillus unilateralis sp. nov.

Coloniae in agaro Czapekii sublanosae, olivaceae, margine albo; reverso in medio paene nigro, margine pallido. Coloniae in agaro maltoso celerius crescentes, lanosae, artemisio-virides, margine albo; reverso in medio viridinigro, margine albo lato; conidiophoris glabris, infimis cellis non densatis; vesiculis 4-8.5 μ; sterigmatibus 6-8 μ in una serie, in vesiculis unilateraliter dispositis; conidiis globosis, 2.5-3.5 μ, echinulatis, hyalinis.

Habitat: in rhizosphaera *Epacridis impressae* Labill. et *Hibbertiae fasciculatae* R. Br.

Colonies on *malt* agar 4 cm in diameter after 14 days' incubation at 24°C. The surface was lanose and coloured artemisia green (XLVII) at the centre, but an overgrowth of trailing hyphae gave a superficial greyish appearance. Beyond the white margin was a band of pale to light glaucous blue (XXXIV). The reverse was greenish slate black (XLVIII) at the centre with a wide white margin.

Colonies on *Czapek's* agar grew more slowly, reaching a diameter of 3 cm in 14 days. The growth was thinner than on malt and the surface less lanose. The centre of the colony was slate olive (XLVII) with the colour fading towards the thin white margin. The reverse was split radially at the centre, where the colour was nearly black, fading to citrine drab (XL) with a paler margin.

On *Raulin's* agar the colony reached a diameter of 3.5-4 cm in 14 days. The surface was somewhat buckled, and the colours resembled those produced on malt. The reverse, which was buckled and split radially, showed some buffy olive (XXX) tones at the centre.

Morphology as on malt agar.—The smooth conidiophores arise from the substrate or from trailing hyphae. They are of variable length, 4-30 μ or more. Over the surface of the vesicle—which measured 4-8.5 μ in width—is borne a single series of widely divergent phialides, 6-8 μ long. The vesicle is set upright upon the conidiophore, but the phialides are arranged irregularly over its surface and the whole presents an eccentric appearance. The number of phialides in the whorl is less than 10, and fragmentary heads are common. The condia are globose, echinulate, 2.5-3.5 μ in diameter.

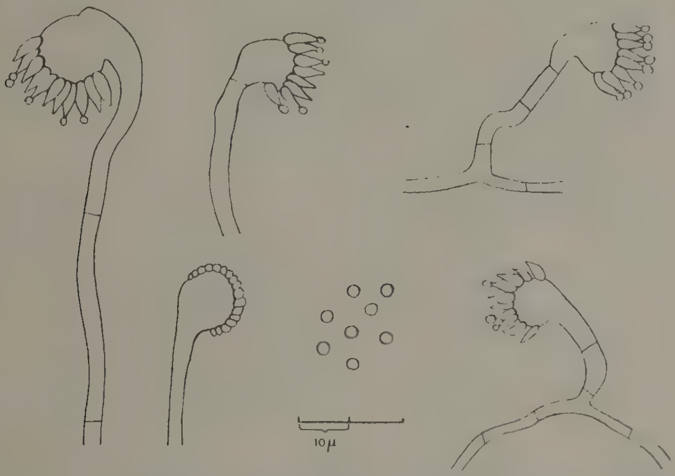


Fig. 2.—*Aspergillus unilateralis* Thrower. Conidial heads and mature conidia. × 385.

This species (No. 2600/27) was isolated from the rhizosphere of *Epacris impressa* Labill. and *Hibbertia fasciculata* R. Br.

A culture has been lodged at the C.M.I.

These three new species of *Aspergillus* have in common:

(1) A single row of phialides.

(2) The globose vesicles, fertile only on the upper half.

(3) Absence of an ascosporic stage, even in freshly isolated colonies.

A. nutans and A. viridi-nutans differ in that the former grows sparsely on Czapek's agar and never produces any sporulating colour on this medium, whereas the latter grows normally. The sporing surface of *A. nutans* is flesh-coloured, while that of *A. viridi-nutans* is green on all media. The two species differ also in spore size, but both have smooth conidia.

A. unilateralis produces the nodding effect, not through a bent conidiophore, but by the eccentric attachment of the phialides, which are also directed in a downward position. The conidia in this species are rough-walled.

According to the natural relationships among the groups of *Aspergilli* as set out by Thom and Raper (1945), our isolates could be compared with the forms placed in the *Aspergillus fumigatus* group in the presence of a single row of phialides situated on the upper half of the vesicle only, but they differ from the species included in this group in the globose vesicle and their nodding habit, and could be segregated into a third series of the *fumigatus* group, for which we suggest the name *Aspergillus nutans* series.

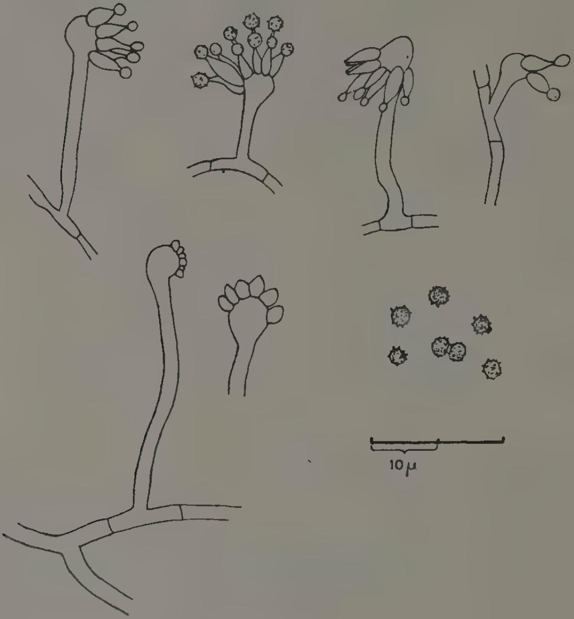


Fig. 3.—*Aspergillus viridi-nutans* Ducker & Thrower. Conidial heads and mature conidia. × 450.

Genus PENICILLIUM Link ex Fr.

Penicillium resedanum sp. nov.

Coloniae in agaro maltoso, celeriter crescentes; fructificationes conidicas abundantes gerentes, funiculos multos efficientes, resedae colorem praebentes, reverso pallido-flavo; coloniae in agaro Czapekii magis restrictae, fornam nidi efficientes, eodem ac supra colore, hyphis flavis in funiculos tortis; conidiophoris, 50-150 μ longis, glabris; penicillis typice monoverticillatis; sterigmatibus paucis, 9-12 μ, lanceolatis apicibus; conidiis ellipticis, 2-3 x 1.5 μ, glabris coloratis.

Habitat: in solo arenoso acido, Australia.

Colonies upon *malt* extract agar spreading broadly 5-6 cm. in 14 days at 24°C with mycelium forming a dense felt. The upper surface is very funiculose, and the overall colour is mignonette green (XXXI) fading towards the edge of the colony to lemon yellow (IV), with a tendency to zonation of colour. The margin of the colony is regular, thin, and white. The reverse of the colony is flat, pale, cream-coloured (XVI) with a buff centre.

Colonies on *Czapek's* agar grow more restrictedly than on malt, attaining a diameter of 2.5 cm in 14 days at 24°C. The funiculose character is more pronounced than on malt; the colonies resemble little nests, the brim formed by a creamy-white lanose growing margin which surrounds the sunken mignonette-green centre. The reverse is cream to avellaneous in the older areas.

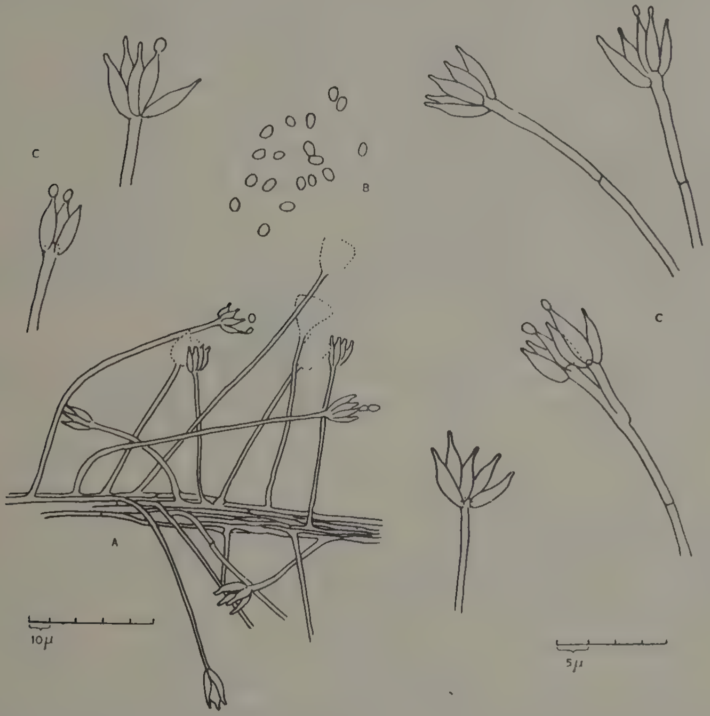


Fig. 4.—*Penicillium resedanum* McLennan & Ducker. *A*, funicles of hyphae with conidiophores. × 200. *B*, mature conidia. × 410. *C*, detailed drawings of penicilli. × 410.

Colonies on *Raulin's* agar grow more rapidly than on Czapek's agar, 4.5 cm in 14 days at 24°C. The nest-like character is more pronounced with a small coloured sunken centre (Kronberg's green XXXI) surrounded by a very lanose white area, 1.5 cm broad, with an abrupt margin. The reverse is slightly buckled, the centre antimony yellow, darkening to yellow ochre in age.

Morphology as on malt agar—The colony is characterized by a profuse development of ropes 10-15 μ wide, consisting of coloured hyphae from which numerous smooth conidiophores arise, 50-150 μ long. Each conidiophore is sparsely septated uniformly 2 μ broad, the apex is slightly swollen and bears a few (3-9) sterigmata; the spore chains are twisted into short columns. The sterigmata which are strongly tapered at their apices are 9-12 by 3 μ. The conidial chains break up readily, the conidia are smooth and tinted broadly elliptical, 2-3 by 1.5-2 μ.

This isolate is a strictly monoverticillate form and produces neither perithecia nor scelerotia, even when newly isolated. The sterigmata are long and tapering, resembling those found in the *biverticillate-symmetrica* series, also the general colour scheme is suggestive of this group. However, we have never found other than monoverticillate conidiophores. The colonies are characterized by the development of prominent funicles or ropes of hyphae, and hence the form must be grouped in the *adametzi* series. It differs, however, from the other forms in that series in the broadly elliptical spores, of the type found in the members of the *lividum* series, but lacks the echinulate character of the spore and the blue-green colour characteristic of the described forms in the *lividum* series. Raper (personal communication, 1954) has examined our isolation and confirmed our view that we are handling a form with features separating it from those species already described. We propose, therefore, to erect a new species under the trivial name *resedanum,* on account of the characteristic mignonette-green colour of the colonies. *Reseda* is the generic name of the mignonette plant.

This *Penicillium* was isolated from the A_1 horizon of the podzol at Frankston, Vic., and a culture (A221) has been lodged at the C.M.I.

Genus SPEGAZZINIA Sacc.

Spegazzinia lobulata sp. nov.

Coloniae in agaro Czapekii velutinae vel floccosae, griseo-virides; reverso nigro. Coloniae in agaro maltoso floccosae, pallido-griseae; mycelio fusco, flavo-viridi, aerio in mediis coloniis; reverso nigro. Conidia duorum generum; alterius generis abundantiora cruciatim 4-cellularia, fusca, 17-22.5 μ longa et lata, 12 μ alta, labulis ornata in conidiophoris 10-15 μ longis, membrana echinulata praeditis; alterius generis in conidiophoris longioribus, 4-cellularia, 20 μ longa et lata, 12.0 μ alta, fusca, spinis longis ornata.

Habitat: in rhizosphaera *Hibbertiae fasciculatae* R.Br.

After 14 days growth on *malt* extract agar at 24°C the colony was 9 cm in diameter, the surface being rather floccose and white to pale grey with yellowish-coloured hyphae at the centre of the colony. Beneath this overlying mycelium was a black basal layer showing marked circular zonation. The reverse was black and zonate. After 4 wk the zonation had disappeared and the surface was less floccose. Small, compact groups of conidia could be seen with the low power of the microscope. The rate of growth was appreciably slower at 18° and 30°; at 10° and 37° it was very slow, and the diameter of the colony was only 1 cm after 14 days.

The same period of incubation on *Czapek* agar gave a colony 5.8 cm in diameter. The central portion of the colony (4 cm) was raised above the surface of the medium; texture was velvety to somewhat floccose and the colour was in green-grey shades. Beyond this region was a very thin, colourless margin about 1 cm wide. The reverse was black and zonate.

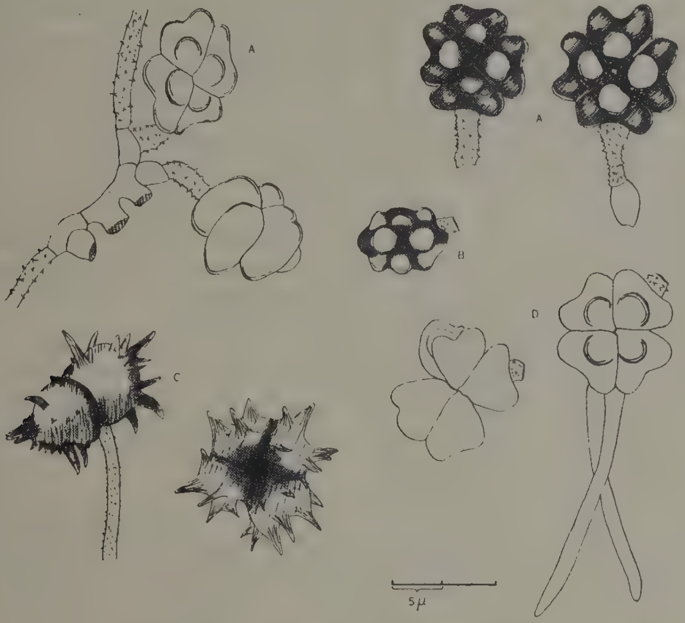


Fig. 5.—*Spegazzinia lobulata* Thrower. *A*, smooth lobulated conidia with their conidiophores. × 385. *B*, same in side view. × 385. *C*, echinulate conidia. × 385. *D*, smooth conidia germinating. × 385.

Morphology as on malt agar.—Conidia of two kinds are produced. The more abundant are borne on conidiophores 10-15 μ long, which are conspicuously rough and arising in small groups. Conidia are cruciately four-celled and measure 17.0-22.5 μ long and wide by 12 μ deep; black when mature, flattened in the plane of the cruciate division, and ornamented with rounded projections on each of the four cells. Each conidium is attached to its conidiophore by the centre of the edge of one of its cells.

The second type of conidia is rounded, four-celled, and bears long spines. The body of the conidium (excluding the spines) measures 20 μ long and wide by 12 μ deep. The conidiophores are longer, but less rough, than those described above; the conidia are attached to the conidiophores at the point of juncture of the four cells.

In his paper elucidating the two spore forms of *S. ornata* Sacc., Bessey (1907) pointed out that some species of *Spegazzinia* form definite sporodochia, whereas others (e.g. *S. trichophila* Atkinson) do not produce them at all. The species described here does not form sporodochia; at most, two or three hyphae form a rope from which small groups of conidiophores arise. This character resembles Dematiaceae more closely than the Tuberculariaceae to which the genus is assigned.

The way in which the smooth conidia are borne is interesting. Generally, a number of conidiophores arise from a definite region of a trailing hypha; whereas the remainder of the hypha is rough, the portion from which the conidiophores arise is smooth. Sometimes the conidium and conidiophore pull away as a whole from the point of attachment, leaving a smooth projection attached to the mother hypha.

The smooth conidia germinated readily in a 2 per cent. solution of malt and, after 16 hr at 24°C the germ tubes varied from 15 to 150 μ long and transverse septa were already present in the longer ones after that period. There was a tendency for each cell to produce a germ tube, though often only one or two were produced per conidium. During germination the conidia frequently separated into their component cells.

According to Mason (personal communication, 1952), the smooth conidia of this species differ from those of the type species, or of other described species, in that they are ornamented with conical or rounded projections. Another difference is the much deeper indentation at the base of each of the four triangular cells.

More recently Damon (1953), in his discussion of *Spegazzinia*, suggested that there is only one good species of this genus—*S. tessarthra* (B. & C.) Sacc. The spores of our species conform with the generic concept, as set out by Damon, but they are smaller than those of the type, and the contour of the smooth-walled spores is irregular, giving to the spores a lobulated appearance; hence the specific epithet "*lobulata*".

This form was isolated from the rhizosphere of *Hibbertia fasciculata* R.Br. and from steamed fallen leaves of *Leptospermum myrsinoides* Schlech. In correspondence with Mr. Mason, of the Commonwealth Mycological Institute, he informed us that Dr. Lilian Frazer had brought to them from Australia in 1937 an identical isolation, but the culture was lost. A culture of *S. lobulata* has been placed at the C.M.I. as C.M.I.49132.

ACKNOWLEDGMENT

For the Latin descriptions we are indebted to Associate Professor H. A. K. Hunt.

REFERENCES

BESSEY, E. A. (1907).—Spore forms of *Spegazzinia ornata* Sacc. *J. Mycol.* **13**: 43-5.

DAMON, S. C. (1953).—Notes on the hyphomycetous genera *Spegazzinia* Sacc. and *Isthmospora* Stevens. *Bull. Torr. Bot. Cl.* **80**: 155-65.

SMITH, G. (1952).—*Aspergillus brevipes* n.sp. *Trans. Brit. Mycol. Soc.* **35**: 241-2.

RAPER, K. B., and THOM, C. (1949).—"A Manual of the *Penicillia*." (Williams & Wilkins Co.: Baltimore.)

THOM, C., and RAPER, K. B. (1945).—"A Manual of the *Aspergilli*." (Williams & Wilkins Co.: Baltimore.)

CORRIGENDUM

VOLUME 2, NUMBER 2

Page 202, lines 29 and 30 only: *For*

Haloragacidites haloragoides n. spm.
Plate 1, Figs. 7-9

read

Haloragacidites myriophylloides n. spm.
Plate 1, Figs. 12-15

INDEX

PAGE

Acacia, The Cainozoic Occurrence of, in Australia .. 52
Agrostological Index, The: A Phytogeographical Approach to the Problems of Pasture Plant Introduction 1
Aluminium Accumulation in the Australian-New Guinea Flora 176
Amos, G. L.—
  Radial Fissures in the Early Wood of Conifers .. 22
Aspergillus, Penicillium, Spegazzinia, New Soil Fungi from Australian Heathland 355
Atriplex, The Leaf Anatomy of Australian Members of the Genus. I. *Atriplex vesicaria* Heward and *A. nummularia* Lindl. 269
Autecology of Some Natural Pasture Species at Trangie, N.S.W. 69

Biddiscombe, E. F., Cuthbertson, E. G., and Hutchings, R. J.—
  Autecology of Some Natural Pasture Species at Trangie, N.S.W. 69
Binet, F. E.—
  See Clifford, H. T. .. 325
Black, R. F.—
  The Leaf Anatomy of Australian Members of the Genus *Atriplex.* I. *Atriplex vesicaria* Heward and *A. nummularia* Lindl. .. 269
Blake, S. T.—
  Botanical Contributions of the Northern Australia Regional Survey. II. Studies on Miscellaneous Northern Australian Plants 99

PAGE

Boronieae, Chromosome Numbers in the, (Rutaceae) and Their Bearing on the Evolutionary Development of the Tribe in the Australian Flora .. 287
Cainozoic Deposits in the Australian Region, Some Dicotyledonous Pollen Types from 197
Cainozoic Occurrence of Acacia in Australia, The .. 52
Chromosome Numbers in the Boronieae (Rutaceae) and Their Bearing on the Evolutionary Development of the Tribe in the Australian Flora 287
Clifford, H. T., and Binet, F. E.—
  A Quantitative Study of a Presumed Hybrid Swarm between *Eucalyptus elaeophora* and *E. goniocalyx* . 325
Cookson, Isabel C.—
  The Cainozoic Occurrence of Acacia in Australia .. 52
Cookson, Isabel C., and Pike, Kathleen M.—
  Some Dicotyledonous Pollen Types from Cainozoic Deposits in the Australian Region 197
  The Fossil Occurrence of *Phyllocladus* and Two Other Podocarpaceous Types in Australia .. 60

PAGE
Corrigendum 267, 365
Crossed Lamellar Structures in the Cell Walls of Higher Plants, Observations on .. 154
Cuthbertson, E. G.—
  See Biddiscombe, E. F. .. 69

Dadswell, H. E., and Ingle, H. D.—
  The Wood Anatomy of New Guinea *Nothofagus* Bl. 141
Ducker, Sophie C.—
  See McLennan, Ethel I. 220, 355

Ecology of the Soil Fungi of an Australian Heathland, The 220
Eucalyptus elaeophora and *E. goniocalyx*, A Quantitative Study of a Presumed Hybrid Swarm between .. 325

Factor Analysis, An Essay in the Use of. Objective Methods for the Classification of Vegetation. III .. 304
Fibres and Tracheids, The Mechanism of Surface Growth Involved in the Differentiation of .. 165
Fissures, Radial, in the Early Wood of Conifers .. 22
Fossil Occurrence of *Phyllocladus* and Two Other Podocarpaceous Types in Australia, The 60
Fungi, Soil, The Ecology of the, of an Australian Heathland 220

Goodall, D. W.—
  Objective Methods for the Classification of Vegetation. III. An Essay in the Use of Factor Analysis .. 304

PAGE
Hartley, W.—
  The Agrostological Index: A Phytogeographical Approach to the Problems of Pasture Plant Introduction 1
Heathland, Australian, New Soil Fungi from 355
  The Ecology of the Soil Fungi of an 220
Heathland Plants, the Rhizosphere Effect Shown by Some Victorian 246
Hutchings, R. J.—
  See Biddiscombe, E. F., and Cuthbertson, E. G. .. 69
Hybrid Swarm, Presumed, A Quantitative Study of a, between *Eucalyptus elaeophora* and *E. goniocalyx* 325

Ingle, H. D.—
  See Dadswell, H. E. .. 141

Jacobs, M. R.—
  The Effect of Wind Sway on the Form and Development of *Pinus radiata* D. Don 35

Leaf Anatomy of Australian Members of the Genus *Atriplex*, The. I. *Atriplex vesicaria* Heward and *A. nummularia* Lindl. .. 269

McLennan, Ethel I., and Ducker, Sophie C.—
  The Ecology of the Soil Fungi of an Australian Heathland 220
McLennan, Ethel I., Ducker, Sophie C., and Thrower, L. B.—
  New Soil Fungi from Australian Heathland: *Aspergillus, Penicillium, Spegazzinia* 355

PAGE

Northern Australian Plants, Miscellaneous, Studies on. Botanical Contributions of the Northern Australia Regional Survey. II. .. 99
Nothofagus Bl., The Wood Anatomy of New Guinea 141

Pasture Species, Natural, Autecology of Some, at Trangie, N.S.W. 69
Penicillium, Spegazzinia, Aspergillus, New Soil Fungi from Australian Heathland 355
Phyllocladus and Two Other Podocarpaceous Types in Australia, The Fossil Occurrence of 60
Phyllotrichia, Sargassum, subgenus, Australian Species of 337
Pike, Kathleen M.—
See Cookson, Isabel C. 60, 197
Pinus radiata D. Don, The Effect of Wind Sway on the Form and Development of 35
Pollen Types from Cainozoic Deposits in the Australian Region, Some Dicotyledonous 197

Rhizosphere Effect Shown by Some Victorian Heathland Plants, The 246
Rutaceae, Chromosome Numbers in the Boronieae .. 287

Sargassum, subgenus *Phyllotrichia,* Australian Species of 337
Smith-White, S.—
Chromosome Numbers in the Boronieae (Rutaceae) and Their Bearing on the Evolutionary Development of the Tribe in the Australian Flora 287
Spegazzinia, Aspergillus, Penicillium, New Soil Fungi from Australian Heathland 355
Surface Growth, The Mechanism of, Involved in the Differentiation of Fibres and Tracheids 165

Thrower, L. B.—
The Rhizosphere Effect Shown by Some Victorian Heathland Plants .. 246
See 355

Vegetation, Objective Methods for the Classification of. III. An Essay in the Use of Factor Analysis 304

Wardrop, A. B.—
Observations on Crossed Lamellar Structures in the Cell Walls of Higher Plants 154
The Mechanism of Surface Growth Involved in the Differentiation of Fibres and Tracheids 165
Webb, L. J.—
Aluminium Accumulation in the Australian-New Guinea Flora 176
Wind Sway, The Effect of, on the Form and Development of *Pinus radiata* D. Don .. 35
Womersley, H. B. S.—
Australian Species of *Sargassum,* subgenus *Phyllotrichia* 337
Wood Anatomy of New Guinea *Nothofagus* Bl., The 141
Wood, Early, of Conifers, Radial Fissures in the .. 22